The Heartfelt Self:

Investigating Interactions between Individual Differences in Interoceptive Accuracy and Aspects of Self-Processing

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Declaration of Authorship

I, Vivien Lesley Ainley, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.

Signed: ………………………………………………….

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Abstract

Recent models of the self accord a key role to ‘interoception’, defined as afferent information arising within the body affecting the behaviour, emotion and cognition of the organism, with or without awareness. The purpose of this thesis was to investigate how individual differences in awareness of internal bodily signals (‘interoceptive accuracy’ (IA), measured by heartbeat perception) relate to two key aspects of self-processing. The first three experiments considered awareness of the self from an exteroceptive perspective, while the second three investigated awareness of the processing of action. Experiments 1 and 2 manipulated IA by enhanced attention to the self. In people for whom IA was initially low, heartbeat perception was improved by self-observation in a mirror, as well as by gazing at a self-photograph and at self-relevant words. Experiment 3 found a significant negative correlation, in women, between self-objectification and IA. Experiment 4 investigated the relationship between IA and the ‘social Simon effect’. No significant effects were found. Experiment 5 found that people with high IA were significantly less able to inhibit imitation during ‘automatic imitation’, potentially because they are more empathetic and thus prone to imitate. Experiment 6 investigated the relation between IA and agency, using time-awareness paradigms pioneered by Libet et al. (1983) and Haggard et al. (2002). A positive correlation was found between IA and ‘intentional binding’, indicating that people with high IA have a stronger sense of agency. The result depended entirely on ‘effect binding’. Replicating recent reports, effect binding was correlated with the amplitude of the early readiness potential in the operant sound condition and also with sensory attenuation. However, IA was not linked to either of these variables. Taken together, the findings reported here provide support for a model of interoceptive accuracy within a predictive coding framework, which is presented in the Discussion.

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Table of Contents

Table of Tables

Chapter 3. Interoceptive Accuracy and the 'Self as Object'

Chapter 4. Interoceptive Accuracy and Self/Other Distinction

Chapter 5. Interoceptive Accuracy and the 'Acting Self'

Appendix Investigating Potential Confounds of Heartbeat Perception

Table of Figures

Chapter 2. The Effect of Enhanced Self-focus on Interoceptive Accuracy

Chapter 4. Interoceptive Accuracy and Self/other Distinction

Chapter 5. Interoceptive Accuracy and the 'Acting Self'

Chapter 6. Discussing Interoceptive Accuracy and Aspects of Self-processing

Appendix. Investigating Potential Confounds of Heartbeat Perception

Chapter 1. Introduction: The Neglected Senses

1.1 Interoception as a Set of Senses

Interoception is defined as the afferent information arising from within the body that affects cognition, feeling states, and the behaviour of an organism, with or without awareness (Cameron, 2002). In contrast to the exteroceptive senses such as vision, audition and somatosensation, interoception is a precognitive, sensory system which is, in most cases, rather vague and difficult to interpret but capable of reaching conscious awareness (Ádám, 2010).

Interoceptive signals arise within four distinct systems - the cardiovascular, respiratory, gastrointestinal and urogenital. Proprioception is also sometimes regarded as an aspect of interoception (Ádám, 2010; Cameron, 2002; Vaitl, 1996) while other authors consider it to be a separate sense (Quattrocki & Friston, 2014) or to be part of somatosensation (Craig, 2003). In the early twentieth century, an extensive body of physiological research, stemming from the work of Eastern European scientists such as Pavlov, identified a variety of 'interoceptor' cells (Sherrington, 1899) defined as structures which detect stimuli within the body (Ádám, 2010; Cameron, 2002; Schandry, 1981; Vaitl, 1996). These have much in common with exterosensory receptors, falling into several classes of mechanoreceptors, chemoreceptors, thermoreceptors and osmoreceptors. Like other sensory signals, afferent signals from the viscera enter the spinal cord through the dorsal horn (Cameron, 2002) and are carried on several major nerves, the most important of which is the vagus. There is a considerable excess of afferent over efferent signalling between the body and the brain, for example, 80% of fibres in the vagus nerve are afferent, conveying information from the viscera to the brain (Ádám, 2010; Critchley et al., 2007). Many of these signals are likely to be engaged in homeostatic regulation of the body. However, some may not be solely homeostatic because they produce sensations that are available to conscious awareness (Ádám, 2010), in striking contrast to deeply unconscious intra-body signals which are engaged only in homeostatic regulation (Panksepp & Northoff, 2009). Pavlov and colleagues were the first to show that interoception is not entirely homeostatic. By directly stimulating interoceptor cells in the mucosa of the internal organs of dogs, they proved that interoception has a direct effect on behaviour and famously showed that these effects could be conditioned (Vaitl, 1996).

Further, often neglected, aspects of interoception are the chemical secretions (hormonal, immunological and metabolic) arising from within the ‘internal milieu’ (Damasio, 2003), which percolate through the body and modulate brain processes (Critchley & Harrison, 2013). Investigation of these neurotransmitters is in its infancy but two studies have reported significant findings. Wiebking and colleagues report that concentrations of GABA in the left insula, which is a convergence zone for interoceptive signals, correlate with BOLD activity during attention to interoceptive cues (Wiebking et al., 2013). By contrast, Ernst et al. found that glutamate concentrations in the left insula correlated with the participants’ self-reported internal body awareness (Ernst, Boker et al., 2013). More recently, the potential role of oxytocin in the interoceptive system has been highlighted (Quattrocki & Friston, 2014).

Interoceptive signalling is often treated as a unitary phenomenon although this assumption is not grounded in the physiology (Vaitl, 1996). It is feasible, for example, that one person’s behaviour or feelings may be principally influenced by changes in their cardiovascular system, while another individual is more affected by changes in signals arising within the respiratory or gastrointestinal interoceptive systems (Cameron, 2002). A further complication is that one interoceptive system might impact on a particular emotion or behaviour (for example, the heart may influence anxiety), while another emotion or cognition could depend on a different set of signals (e.g. feelings of disgust may depend on signals from the gastrointestinal interoceptive system). It is even possible that someone more innately attuned to sensations from their heart could experience some emotions (perhaps fear and love) with greater intensity than another individual who has a stronger interoceptive representation of the functioning of their stomach (Critchley, 2009). However, until a variety of tests in different modalities are developed, such possibilities remain speculative.

1.2 ‘Interoceptive Accuracy’

Individuals differ in the extent to which they are aware of their internal bodily cues. There are, however, a number of potential confusions in defining and measuring this trait. The terms ‘interoceptive sensitivity’ and ‘interoceptive awareness’ are often used interchangeably to describe how individual differ in terms of interoceptive sensation but they are not necessarily synonymous. If an individual has high ‘interoceptive sensitivity’ this seems to imply that the person’s cognition, feelings and/or behaviour are strongly influenced by signals arising within the body, regardless of whether this is accompanied by conscious awareness. ‘Interoceptive awareness’, on the other hand, implies reference to the individual’s conscious awareness of (at least a part) of their interoceptive cues. The assumption is generally made that interoceptive awareness implies interoceptive sensitivity because when people are aware of their internal cues (such as breathlessness or a racing heart) it is probable that this impacts on their behaviour, feelings and/or cognition. The converse may not necessarily be true, in that the emotional reactions of individuals might be highly sensitive to their visceral changes without the person having any conscious awareness of those internal bodily signals.

Further definitional difficulties are raised by the many self-report body awareness measures which have been used either in place of, or in addition to, physiological measures of interoceptive awareness/sensitivity (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Ernst, Boker, et al., 2013; Terasawa, Shibata, Moriguchi, & Umeda, 2013). People’s beliefs about how accurately they are aware of their internal body signals often do not correlate with their performance on objective tests (Cuenen, Van Diest, & Vlaeyen, 2012). For example, experienced meditators, such as Buddhist monks, believe themselves to have high internal body awareness but are not more accurate than controls in heartbeat perception (Khalsa et al., 2008). Similarly, although Mindfulness training (Williams, 2010) raises peoples’ confidence in their body awareness, it does not change their scores in cardiac awareness tests (Parkin et al., 2013). Recently, Garfinkel and colleagues have suggested that ‘interoceptive accuracy’ should be the term for scores on objective tests, ‘interoceptive sensibility’ for self-report measures and that ‘interoceptive awareness’ should be reserved for metacognitive measures. They report that these measures correlate in individuals with above median performance on heartbeat perception tasks but not in people with below median accuracy (Sarah N Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2014).

The term ‘interoceptive accuracy’ has been used throughout this thesis to refer to scores on the Mental Tracking Method of heartbeat perception (Schandry, 1981).

1.2.1 Methods of Assessing Individual Differences in Interoceptive Awareness

Techniques originally pioneered by Pavlov and co-workers to assess this ‘visceroception’ included highly invasive procedures in animals (and sometimes in humans who were undergoing surgery), such as the insertion of inflatable balloons into the gut or the direct stimulation of the mucosa of the viscera with saline, or air puffs, or by scratching (Ádám, 2010). The use of non-invasive heartbeat perception tests became the standard method of measuring awareness of interoceptive sensations in humans after a significant correlation was found between an individual’s accuracy in heartbeat perception and their awareness of the irrigation of their stomach wall with water (Whitehead & Drescher, 1980). When new tests of the awareness of interoceptive sensations are proposed, the acid test of their validity is judged to be the extent to which they correlate with accuracy in heartbeat perception (Harver, Katkin, & Bloch, 1993; Herbert, Muth, Pollatos, & Herbert, 2012). It is, however, not clear what people are detecting when they count their heartbeats (Verdejo-Garcia, Clark, & Dunn, 2012). It may be auditory cues or perhaps blood flow in the aorta or elsewhere in the vasculature (Cameron, 2002). Two recent studies have suggested that mechanical sensation in the chest wall provides a path of awareness (Couto et al., 2013; Khalsa, Rudrauf, Feinstein, & Tranel, 2010). Despite these caveats, research into the cognitive, emotional and behavioural effects of the awareness of interoceptive sensation, measured in terms of heartbeat perception, has proved surprisingly fruitful (Cameron, 2002).

The research literature is divided between studies that use heartbeat tracking tasks (McFarland, 1975; Schandry, 1981), of which the Mental Tracking Method pioneered by Schandry (1981) is the most prominent test, and those that employ heartbeat discrimination methods (Brener & Jones, 1974; Whitehead & Drescher, 1980).

The Mental Tracking Method (Schandry, 1981) is the most widely used heartbeat tracking task. The participant is connected to a pulse recorder and required to sit quietly for a few minutes, in order to allow her heart to return to resting rate, thus avoiding confounds caused by arousal. The individual is then asked to count her heartbeats for several cued, short intervals (typically at least three trials of between 25s and100s), simply by 'listening' to her body, without taking her pulse (Schandry, 1981). In order to obtain a measure of accuracy for any given trial, the number of counted heartbeats is compared with the number of recorded beats using the formula 1- (|recorded heartbeats – counted heartbeats|)/recorded heartbeats). Averaging across trials produces a single numerical measure for 'interoceptive accuracy' (IA). This calculation generally produces a score between zero and one, with higher values indicating greater accuracy. Most people count too few heartbeats but values of IA greater than one are theoretically possible in instances where participants greatly overestimate the number of counted beats.

Heartbeat discrimination tasks are generally variants of the Whitehead paradigm (Whitehead & Drescher, 1980) in which subjects listens to a series of tones (or, in the visual paradigm, see a series of flashes) triggered by their own heartbeat. During 'simultaneous' trials, tones are delivered at the same time as the subject's own pulse, i.e. approximately 200–250ms after the R-wave because the pulse is typically felt with a short delay. During 'non-simultaneous' trials, tones are delivered approximately 500–700ms after the R-wave. Individuals must judge whether the tone they hear is simultaneous with their own heart. Responses can be analysed using signal detection methods. A non-parametric analogue of d′ is sometimes calculated (where $d' = z_{\text{hit rate}} - z_{\text{false alarm rate}}$) but participants are often simply divided into 'good' and 'poor' heartbeat detectors on the basis of whether they score above chance. Heartbeat discrimination tasks have the unfortunate disadvantage that the majority of people score below chance, so that these tests do not provide a sensitive measure of individual differences (Eshkevari, Rieger, Musiat, & Treasure, 2014). A further important criticism of tests based on the Whitehead paradigm is that they require participants to correlate an exteroceptive stimulus (e.g. an auditory tone) with an interoceptive signal (the heartbeat). The task may not therefore be measuring interoceptive awareness *per se* because when attention is directed outwards to the tone, exteroception potentially inhibits interoception (Ádám, 2010; Pennebaker & Lightner, 1980). Moreover, people may perform well on the Whitehead paradigm without conscious awareness of their heartbeats, so that the test potentially assesses ‘interoceptive sensitivity’ rather than conscious ‘interoceptive awareness’ or ‘interoceptive accuracy’. A significant consequence is that the two types of methods do not necessarily assess the same ability (Phillips, Jones, Rieger, & Snell, 1999; Schulz, Lass-Hennemann, Sütterlin, Schächinger, & Vögele, 2013).

1.2.2 Correlation between the Two Common Heartbeat Perception Methods

The most commonly cited reference for correlation between the Whitehead and Schandry methods found an overall coefficient of .59, with better correlation for very good and very poor perceivers but less good correlation for those in the middle range of accuracy (Knoll & Hodapp, 1992). A recent study of chest pain, suggests a smaller but significant correlation (.28) between the two methods but did not distinguish between cardiac patients, those with symptoms of somatic origin and controls (Schroeder, Gerlach, Achenbach, & Martin, 2014). Garfinkel and colleagues recently found a correlation of .32 (Sarah N Garfinkel et al., 2014) but other sources have reported that scores on the two methods are largely unrelated (Michal et al., 2014; Phillips et al., 1999; Schulz et al., 2013). An additional indication that the two tests potentially measure different abilities is provided by Schulz and colleagues. They reported that performance on the Whitehead task decreased following a socially evaluated cold pressor task, while accuracy in Mental Tracking was significantly improved. If the Whitehead task requires attention to external auditory or visual stimuli, this attention potentially declines when interoceptive signals are made salient by the cold pressor, while if the Mental Tracking Method is purely interoceptive then attention to interoceptive cues could boost performance (Schulz et al., 2013).

1.2.3 Correlations with Other Modalities of Interoceptive Awareness

Although heartbeat perception methods predominate in the literature, a few attempts have been made to test awareness of interoceptive sensations in other modalities. Ingestion of water during the Water Load test, correlates (*r* = -.5), with interoceptive accuracy measured by the Mental Tracking Method (Herbert, Muth, et al., 2012). A similar correlation (*r* = .51) was reported by Whitehead and Drescher between patients' ability to discriminate their heartbeat and their awareness of the irrigation of their stomach wall with water (Whitehead & Drescher, 1980). However, the ability to detect respiratory resistance, using small meshes to occlude breathing, is uncorrelated with heartbeat perception measured by the Whitehead method (Harver et al., 1993), perhaps because the Whitehead method does not discriminate adequately between individuals.

1.2.4 Confounds of Heartbeat Perception Tasks

All heartbeat perception tasks are confounded by cardiovascular variables. People with high blood pressure (Koroboki et al., 2010) and/or larger stroke volume of the heart have an advantage, as do those with slow resting heart rates and high levels of fitness, probably because heart rate and fitness correlate with stoke volume (Fairclough & Goodwin, 2007; Knapp-Kline & Kline, 2005; Stevens et al., 2011). For example, using the Mental Tracking Method, Schandry reported a correlation of .59 between heartbeat perception and stroke volume (Schandry, Bestler, & Montoya, 1993). One report suggests that low heart rate variability is associated with good heartbeat perception, perhaps because less variable hearts are easier to follow (Knapp-Kline & Kline, 2005). Men are thought to perform better (Brener & Ring, 1995; Katkin, Blascovich, & Goldband, 1981), potentially because they have larger hearts, but this may also be related to body mass index (BMI), because leaner people are more accurate (Jones, 1995) and women tend to have more body fat. It has also been reported that heartbeat discrimination measured by the Whitehead method declines with age (Khalsa, Rudrauf, & Tranel, 2009), although this might reflect a decline amongst older people in the ability to integrate auditory and interoceptive signals. A serious disadvantage of the Mental Tracking Method is, however, that participants may correctly guess the number of heartbeats, based on their estimation of the time elapsed. A control for this confound is provided by requiring participants to estimate the length of several elapsed intervals and adding their accuracy in time estimation into regression equations involving interoceptive accuracy (Dunn et al., 2010; Ehlers & Breuer, 1992; Ring & Brener, 1996).

1.2.5 Test Retest Reliability

The Mental Tracking Method has good test retest reliability, with published correlations coefficients of between .58 (Mussgay, Klinkenberg, & Rüddel, 1999) and .80 (Werner, Kerschreiter, Kindermann, & Duschek, 2013). Similar levels of test retest reliability have been reported for the Whitehead method (Schneider, Ring, & Katkin, 1998).

The Mental Tracking Method (Schandry, 1981) was employed in all the experiments presented in this thesis because it is the test that discriminates best between individuals. It also requires that participants only attend to their interoceptive cues, without attempting to match these against exteroceptive stimuli.

1.2.6 Interoceptive Accuracy as a Continuous Variable

Although interoceptive accuracy is a continuous variable, much research using heartbeat perception paradigms has concentrated on individuals with high interoceptive accuracy. Using the Schandry formula for interoceptive accuracy in Mental Tracking (where 1 represents a perfect score in counting one's heartbeat), it has been common to designate people with scores greater than 0.85 as 'good heartbeat perceivers' (Herbert, Pollatos, & Schandry, 2007; Pollatos, Herbert, Matthias, & Schandry, 2007; Pollatos & Schandry, 2008; Werner, Jung, Duschek, & Schandry, 2009). This enables comparison with the few people who score above chance on the Whitehead task (Eshkevari et al., 2014; Harver et al., 1993; Katkin, Wiens, & Ohman, 2001; Khalsa et al., 2008; Wiens, 2005). In many studies, the group with interoceptive accuracy above 0.85 is matched for BMI, gender and other relevant confounding variables with a group of 'poor heartbeat perceivers' and the mean behaviour of the two groups is compared on the dimension under test. Such studies have reported significant differences between groups with 'high' and 'low' interoceptive accuracy on a range of variables, including autonomic reactivity in response to stress, the amplitude of heartbeat-evoked potentials and the ability to divide attention (Herbert, Pollatos, Flor, Enck, & Schandry, 2010; Matthias, Schandry, Duschek, & Pollatos, 2009; Pollatos & Schandry, 2004).

However, a series of recent experiments using the Mental Tracking Method have analysed data using a median split and shown that low interoceptive accuracy is also important. In these experiments, it is the participants with below-median interoceptive accuracy who have often responded significantly to the experimental condition. For example, people with low interoceptive accuracy experience a stronger rubber hand illusion (Tsakiris et al., 2011). Similarly, in the enfacement illusion, where people judge another person’s face as significantly more like their own after synchronous brushing, it is the people with below median accuracy in heartbeat tracking who demonstrate increased electrodermal activity when the other face is threatened (Tajadura-Jiménez & Tsakiris, 2013).

Throughout this thesis the full range of individual differences in interoceptive accuracy has been considered, in order to investigate the effect of low as well as high accuracy.

1.3 Interoceptive Accuracy as a Trait Variable

Interoceptive accuracy has generally been regarded as a trait variable because attempts to alter heartbeat perception are usually unsuccessful, except where arousal is increased. Techniques that involve relaxation and attention to the body, for example through Yogic breathing patterns or Mindfulness training, do not alter scores on objective tests (Fairclough & Goodwin, 2007; Khalsa et al., 2008; Parkin et al., 2013). However, social evaluation can increase the accuracy of heartbeat perception. A cold pressor test in the presence of an attractive member of the opposite sex (Schulz et al., 2013) or the anticipation of public speaking (Durlik, Brown, & Tsakiris, 2013) raises performance on the Schandry task (but see also Stevens et al., 2011). Likewise, an early study found that the apparently accidental presence of a mirror improved performance on the Whitehead test, although not on a heartbeat tracking task (Weisz, Bálazs, & Ádám, 1988). These results suggest that attention to higher order aspects of ‘the self’ may improve performance on heartbeat perception tests. This echoes the theory of ‘objective self-focus’ (Duval & Wicklund, 1972) which proposes that enhanced attention to the self is inherently aversive. Given these intriguing findings, the possible influences on interoceptive accuracy of enhanced self-focus and narrative aspects of the self merit further investigation and were therefore the subject of Experiments 1 and 2 of this thesis.

1.3.1 The Effect of Attending to Interoception

The importance of attentional processes for the awareness of interoceptive sensation has perhaps been insufficiently emphasised (Ádám, 2010; Vaitl, 1996). A study of attention and interoceptive accuracy, using the Mental Tracking Method, found that people with high interoceptive accuracy performed better in tests of selective and divided attention (Matthias et al., 2009), implying that the ability to switch attention potentially underlies good heartbeat perception. The suggestion that interoceptive accuracy is a function of attentional mechanisms has considerable explanatory power.

According to the ‘competition of cues’ hypothesis (Pennebaker & Lightner, 1980), the organism must continually divide its limited attentional resources between interoceptive and exteroceptive stimuli, with the urgent survival need of attending to exteroceptive cues generally suppressing attention to interoception (Ádám, 2010). Successful heartbeat perception requires that subjects turn their attention inward, to the very best of their ability, while ignoring exteroceptive distractors. Several fMRI studies have investigated the neural correlates of switching attention between interoceptive and exteroceptive signals and report changes in areas that are thought to be associated with self-processing, including the anterior insula and the ventromedial prefrontal cortex (Farb, Segal, & Anderson, 2012; Nagai, Critchley, Featherstone, Trimble, & Dolan, 2004; Terasawa et al., 2013).

The effects of attention to internal cues can also be seen in experiments that are not inherently concerned with the measurement of interoceptive accuracy but which nevertheless ask participants to count their heartbeats and compare the effect of this manipulation with counting exteroceptive tones. When attention is directed to interoceptive cues in this way, it impacts on cognition and behaviour, for example by enhancing fear conditioning or the judgement of emotion in faces (Ernst, Northoff, Böker, Seifritz, & Grimm, 2013; Raes & De Raedt, 2011). Likewise, when people are played their own heartbeats, in contrast to other rhythmic sounds, this influences their behaviour in the Ultimatum Game, most probably by enhancing attention to interoceptive cues (Lenggenhager, Azevedo, Mancini, & Aglioti, 2013).

The effect of attention to interoceptive signals is also evident from the study of heartbeat-evoked potentials, which appear during EEG as a positive potential shift, around 250-600ms after the R-wave. The height of the heartbeat-evoked potential at central scalp locations correlates positively with scores on the Mental Tracking Method (Pollatos & Schandry, 2004) and, in common with interoceptive accuracy, heartbeat-evoked potentials are influenced by cardiac parameters (Schandry & Bestler, 1995). Heartbeat-evoked potentials have sometimes been regarded as a proxy for interoceptive representation because they reflect the brain's increased sensitivity to bodily states when assessing emotion (Fukushima, Terasawa, & Umeda, 2011). For example, both interoceptive accuracy and heartbeat-evoked potentials are reduced in depressed patients (Terhaar, Viola, Bär, & Debener, 2012). However, although increased attention to heartbeats increases the amplitude of heartbeat-evoked potentials, it does not improve accuracy in heartbeat perception (Montoya, Schandry, & Müller, 1993; Schandry & Weitkunat, 1990), suggesting that attention to interoception is probably at ceiling in the Schandry task. Potentially, therefore, what is being measured by Mental Tracking is the limits of the individual's ability to turn their attention inward. This may be the most useful way to characterise the awareness of interoceptive sensation.

A prominent means of conceptualising the self within social psychology is based on 'objective self-awareness' (Duval & Wicklund, 1972) whereby the individual takes a third-person perspective and consider themselves as the object of their own and other people's thoughts. In this tradition it is assumed that turning attention onto the self enhances the accuracy with which people make judgments about all aspects of self (Silvia & Gendolla, 2001). This 'perceptual accuracy hypothesis' has rarely been subject to controlled testing. Thus, whether enhanced self-focus can improve interoceptive accuracy has not yet been established.

It has also been suggested (Wheeler, Morrison, DeMarree, & Petty, 2008), that a tendency to direct attention inwards is correlated with trait 'private self-consciousness' (Fenigstein, Scheier, & Buss, 1975). If so, this implies a link with interoceptive accuracy. Relationships between body awareness and self-consciousness have been studied in social psychology, using self-report measures, but awareness of interoceptive sensations, assessed by physiological measures such as heartbeat perception, have rarely been considered within this research (Mehling et al., 2009).

1.3.2 Links between Interoceptive and Exteroceptive Awareness

The competition of cues hypothesis (Pennebaker & Lightner, 1980) predicts that there will be negative associations between awareness of interoceptive cues and awareness in other sensory modalities. The results of several studies support this proposal. Interoceptive accuracy, measured by Mental Tracking, correlates with the threshold of olfactory detection, $r = .55$ in controls and $r = .40$ in those with acquired impairments in olfaction (Krajnik, Kollndorfer, Notter, Mueller, & Schöpf, 2014). In patients, disease duration and the threshold of olfaction together explained 35% of the variance in interoceptive accuracy, suggesting that as people lose their sense of smell they become less able to access interoceptive cues. Perhaps their attention becomes increasingly turned outwards as their disease progresses and olfaction becomes more effortful, resulting in less available attention for interoception. The results of a somatic detection task may be similarly interpreted. Following several minutes of counting their pulse, relayed to their fingertips, participants had a more liberal criterion for reporting touch (Mirams, Poliakoff, Brown, & Lloyd, 2012). The authors concluded that heightened attention to interoception leads to the reporting of illusory symptoms but an alternative, competition of cues, interpretation would be that a period of attending to interoceptive cues temporarily reduced the accuracy of somatosensory perception. Durlik and colleagues found that heightening attention to the exteroceptive representation of the participant's body (by use of a video camera), significantly improved hit rate and sensitivity on a somatic detection task. This suggests that when people attend exteroceptively their accuracy in detecting somatosensory cues improves, however, the expected corresponding reduction in interoceptive accuracy was not observed (Durlik, Cardini, et al., 2014).

Potential links between pain and interoceptive accuracy have also been studied. Pain has somatosensory aspects (Avenanti, Bueti, Galati, & Aglioti, 2005), where competition of cues would predict a negative association with interoceptive accuracy. However, the equally crucial affective dimension of pain (Singer et al., 2004) will be represented interoceptively, suggesting that high interoceptive accuracy could be associated with greater experience of pain. It has been reported that thresholds for the somatosensory pain of thermal stimulation do not correlate with scores on the Mental Tracking task (Horing, Kugel, Brenner, Zipfel, & Enck, 2013; Werner, Duschek, Mattern, & Schandry, 2009) and nor does the visceral pain of rectal balloon distension (Horing et al., 2013). However, using cutaneous pressure and with heart rate variability analysis to distinguish sympathetic and parasympathetic changes, Pollatos and colleagues reported lower thresholds, as well as lower pain tolerance, in people with high interoceptive accuracy, measured by the Mental Tracking Method (Pollatos, Füstös, & Critchley, 2012).

In a fascinating new development, heartbeat perception has been compared with error monitoring during the Simon task (Sueyoshi, Sugimoto, Katayama, & Fukushima, 2014). On trials where the participants made mistakes, accuracy in the Mental Tracking task correlated with the amplitude of the error-positivity, which is a late component of error-related neural processing, observable under EEG. Heartbeat perception was also correlated with the increase in reaction times that occurs on trials immediately after an error has been detected. Error related components and post-error slowing are thought to originate in the anterior cingulate cortex (van Veen & Carter, 2006) and have been linked to measures of empathy (Larson, Fair, Good, & Baldwin, 2010) The authors interpret their results as indicating that the monitoring of inner bodily states and the monitoring of behaviour are related. An alternative explanation is that the affective consequences of making errors is greater in people with higher interoceptive accuracy, who generally report more emotional arousal as well as more anxiety. Such an explanation relies on the well-established links between interoception and emotion.

1.4 Defining Emotion in terms of Interoception

1.4.1 Interoceptive Accuracy and Emotion

Until relatively recently, research into the awareness of interoceptive sensation has been almost exclusively concerned with the interoceptive underpinnings of emotion, based originally on the James-Lange theory of emotion (James, 1890). William James proposed a visceral sensorimotor theory of emotion, tightly linked to interoception. Any animal that moves has options and needs action plans which can be adapted by learning (Damasio, 2010; Panksepp & Northoff, 2009). Emotions provide these action plans through physiological, behavioural and ‘feeling’ components (Cameron, 2002; Harrison & Critchley, 2007). In James’s theory, it is the conscious readout of the otherwise unconscious interoception that adds the ‘feelings’ to human emotions. He famously suggested that we see a bear (a percept) and we run (elicited behaviour) but only afterwards do we humans consciously feel the fear, which is the readout of the peripheral bodily reactions (James, 1890). James's insight that an emotion is a reflection in the brain of the state of the viscera has been highly influential.

The links between interoception, emotion, cognition and behaviour were elaborated by Damasio in his 'somatic marker hypothesis' (Damasio, 1996). He postulated the existence of an evolutionarily ancient mechanism that attaches an emotional memory or 'marker' to an external stimulus, based on the organism's bodily reactions to the stimulus. It is now accepted that interoception provides the mechanism for the crucial links between the individual's (largely unconscious) bodily reactions and the effect that these body signatures have on the judgements and choices that the person makes (Dunn, Dalgleish, & Lawrence, 2006). The somatic marker hypothesis therefore provides a description of the way in which interoception affects cognition and behaviour, with or without conscious awareness (Cameron, 2002).

The extent to which people's choices are influenced by their somatic markers depends on their interoceptive accuracy (Werner, Jung, et al., 2009). Typical analysis compares groups of subjects with high and low interoceptive accuracy. However, Dunn and colleagues using the whole range of interoceptive accuracy and measured participants' arousal to emotional pictures both objectively (through heart rate change and skin conductance) and subjectively (by self-report). They found that interoceptive accuracy (measured by Mental Tracking) moderated the relationship between these measures of objective and subjective arousal, such that people with high interoceptive accuracy reported higher arousal than people with low interoceptive accuracy, despite having identical objective changes in physiological variables (Dunn et al., 2010). Importantly, the extent to which individuals' choices in an intuitive decision making task (a variant of the Iowa Gambling Task) were then influenced by these 'somatic marker' depended on their interoceptive accuracy. Individuals with high interoceptive accuracy were inclined to follow their intuition (making decisions that were congruent with the changes in their heart rate and skin conductance), even when they were in error. Dunn et al.'s study importantly demonstrates that what varies between individuals is not actual changes in bodily signals but the extent to which these interoceptive changes impact on an individual’s feelings, cognitions and behaviour.

A similar explanation would account for the report that people with high interoceptive accuracy are more susceptible to ‘framing effects’ when making risky decisions (Sütterlin, Schultz, Stumpf, Pauli, & Vogele, 2013). It is probable that interoceptive accuracy indexes the extent to which the emotional/interoceptive responses to the frames affect decision making in this task.

There is a wealth of evidence indicating that individuals with higher awareness of interoceptive sensation (measured by heartbeat perception) experience more emotional arousal than those with lower awareness, despite similar objective physiological responses (Dunn et al., 2010; Pollatos, Herbert, et al., 2007; Wiens, Mezzacappa, & Katkin, 2000). People with high interoceptive accuracy also demonstrate more ‘arousal focus’, using words implying strong activation when describing their emotions (Barrett, Quigley, Bliss-Moreau, & Aronson, 2004). Similarly, strong P300 waves (a mark of emotional processing), as well as greater self-reported arousal, have been reported in people with high interoceptive accuracy in response to emotional pictures (Herbert, Pollatos, et al., 2007; Pollatos, Kirsch, & Schandry, 2005). This positive link between interoceptive sensation and emotional arousal is in accordance with theories that interoception underpins all emotional experience (Craig, 2004; Damasio, 2003a; James, 1890; Seth, 2013). Potentially, people who are more aware of interoceptive sensations are therefore more powerfully aware of their emotions, thus experiencing greater emotional arousal. Generally, no differences in the valence of the emotion are found.

Further evidence for the role of interoception in emotion is provided by patients with peripheral autonomic de-enervation, who are unable to modulate their body state through the autonomic system because of degeneration of peripheral ganglion cells. They show no changes in heart rate or skin conductance under stress or when processing emotion. Such patients have less activity in the insula and amygdala during fear conditioning, demonstrating that their lack of interoceptive signals directly reduces their experience of fear (Critchley, Mathias, & Dolan, 2002).

Interoceptive accuracy similarly affects emotional memory, presumably because all memories have interoceptive content, as implied by the somatic marker hypothesis (Pollatos & Schandry, 2008; Werner, Peres, Duschek, & Schandry, 2010). The unconscious effect of interoception on emotional memory is powerful evidence for the role of interoception in cognition and behaviour, showing that implicit emotional learning is moderated by interoceptive accuracy. In a further important study, participants were non-consciously fear-conditioned with pictures of snakes and spiders, paired with mild electric shocks (Katkin et al., 2001). Individuals classed as good heartbeat detectors on the Whitehead task were able to predict, above chance, which pictures would be accompanied by shocks, despite being unable consciously to detect the images. This type of fear conditioning is also enhanced by attention to interoception (Raes & De Raedt, 2011).

Cardiac timing is known to influence perceptual processing. For example, the effect on muscle sympathetic nerve activity of mild electrical stimulation differs depending on where is it presented relative to the R wave of the heartbeat (Donadio, Kallio, Karlsson, Nordin, & Wallin, 2002; Gray, Rylander, Harrison, Wallin, & Critchley, 2009). Recent studies have begun to unravel the extent to which this type of effect is modulated by heartbeat perception (Garfinkel et al., 2013). Baroreceptors are the pressure and stretch receptors in the major arteries emerging from the heart, which convey information to the brain about the physiological level of arousal. They play a major role in cardiac homeostasis by setting blood pressure and modulating autonomic responses (Gray et al., 2009). Garfinkel and colleagues showed that emotional words are less well remembered if they are presented when the heart is at systole (a state of physiological arousal, when the baroreceptors are firing) rather than at diastole. Importantly, this effect is less pronounced in people with high interoceptive accuracy (measured by Mental Tracking). Moreover, people with high interoceptive accuracy can correctly recall the presented words, despite having lower confidence in the accuracy of their recall (Garfinkel et al., 2013). The authors suggest that the accuracy of interoceptive representations in good heartbeat perceivers mitigates the deleterious effect of physiological arousal on emotional memory.

An important consequence of the relationship between interoception and emotional experience is that interoceptive accuracy has implications for emotional disorders.

1.4.2 Interoceptive Accuracy in Clinical Disturbances of Emotion

Research into the links between interoceptive sensation and emotion has been fuelled by attempts to relate high awareness of interoceptive sensation to clinical conditions - principally to anxiety. A large body of research suggests that high awareness of interoception is associated with anxiety (Domschke, Stevens, Pfleiderer, & Gerlach, 2010). However, significant links are generally found only in studies which measure interoceptive accuracy using the Mental Tracking Method. Panic is an anxiety disorder involving high arousal, where patients often catastrophise about normal interoceptive sensations (Clark, 1986). High interoceptive accuracy may be a predisposing factor and many researchers have investigated this relationship (Ehlers & Breuer, 1992; Van der Does, Antony, Ehlers, & Barsky, 2000) but with mixed results (Ehlers et al., 1995). Links between interoceptive accuracy and depression are even less clear-cut (Critchley et al., 2004; Dunn, Lawrence, & Ogilvie, 2007; Terhaar et al., 2012), probably because the relationship between interoceptive accuracy and, frequently comorbid, anxiety and depression depend on complex interactions (Dunn et al., 2010; Pollatos, Traut-Mattausch, & Schandry, 2009).

There are, however, advantages to having high interoceptive accuracy. Good heartbeat perceivers are better able to down-regulate unpleasant emotion (Füstös, Gramann, Herbert, & Pollatos, 2012), exhibit less reaction to social inclusion (Werner et al., 2013) and have higher emotional intelligence (Schneider, Lyons, & Williams, 2005). People with high interoceptive accuracy are also more able to self-regulate their behaviour to cope with increased physical load (Herbert, Ulbrich, & Schandry, 2007).

Abnormally low interoceptive accuracy is now recognised as equally problematic. In patients with alexithymia (defined as difficult in identifying and characterising emotional experiences), symptom severity is inversely related to heartbeat perception (Herbert, Herbert, & Pollatos, 2011). People with health anxiety potentially have low interoceptive accuracy (Krautwurst, Gerlach, Gomille, Hiller,

& Witthöft, 2014) as do sufferers from depersonalisation disorder (Sedeño et al., 2014) and those with personality disorders and psychosomatic complaints (Mussgay et al., 1999; Pollatos et al., 2011). However, a recent study of patients with cardiac pain of somatic origin found no difference in their heartbeat perception compared with controls, although scores on the Mental Tracking Task correlated with the distress associated with their pain (Schroeder et al., 2014).

It is possible that many such patients' symptoms result from misreading of interoceptive signals. Both depression and addiction have been linked to insula dysfunction, which could indicate deficits in interoception (Naqvi & Bechara, 2009; Wiebking & Northoff, 2014). Likewise the blunted autonomic reactivity reported in somatoform patients suggests that faulty interoceptive signalling may underlie this condition (Pollatos et al., 2011). Sufferers from anorexia nervosa and bulimia, as well as obese people, have lower interoceptive accuracy than controls - potentially reflecting their inability to accurately perceive the homeostatic interoceptive signals that set normal appetite (Herbert & Pollatos, 2014; Klabunde, Acheson, Boutelle, Matthews, & Kaye, 2013; Pollatos et al., 2008). By contrast, intuitive eating is associated with good interoceptive accuracy (Herbert, Blechert, Hautzinger, Matthias, & Herbert, 2013). Current longitudinal research on eating behaviour, body weight and interoceptive accuracy in children may, over time, elucidate the development of such disorders (Koch & Pollatos, 2014).

Research into links between personality variables and interoception may also throw light on both normal and clinically disturbed experience of emotion. It has recently been shown that during attention to interoceptive cues (heartbeat counting) BOLD activity in the right anterior insula (the principal convergence zone for interoceptive signals) is positively related to neuroticism but negatively associated with extraversion, agreeableness and openness to experience (Terasawa et al., 2013).

1.5 Defining the Self with respect to Interoception

By contrast with the wealth of studies linking interoceptive accuracy with emotion, relatively little empirical attention has been devoted to the role of interoception in underpinning feelings of selfhood, although this idea also has a history that can be traced to William James (James, 1890). The aim of this thesis was to address aspects of this gap in the literature. The shortage of research in this area is particularly surprising, given that the purpose of the existence of any organism is to preserve its own life, while enhancing its reproductive success (Ádám, 2010; Friston, 2013), and that to achieve this it must rely on interoceptive signalling. It is the interoceptive state of the body that crucially dictates how an animal will interact with the world, as well as the affective significance it will attach to objects, including other organisms (Damasio, 2010). Potentially, the sense of self may have evolved in order to unify interoceptive consequences - vital to survival - and to link them with the actions and perceptions that provoke them (Craig, 2010; Damasio, 2010). As a theoretical proposal, this account of the self has been the subject of considerable discussion. Several recent definitions have consequently taken as a starting point the assumption that the evolution of the self developed out of processes of life regulation and homeostasis. Such models propose that the body is the foundation of the conscious mind (Craig, 2010; Damasio, 2010; Park & Tallon-Baudry, 2014; Seth, 2013) and that interoception provides two crucial linked roles (Damasio, 2010; Panksepp & Northoff, 2009). Firstly, interoception underpins the fundamental feelings that we exist. Secondly, interoception is the basis of all emotion (as described in Section 1.3.2). Emotion, however, is itself intrinsically self-referencing, being concerned with furthering the survival and success of the organism (LeDoux, 2012), so that these two roles of interoception are essentially linked. The assumption in which this thesis is grounded, that the self relies on interoceptive processing, has been explored in a number of recent theoretical models of the self.

1.5.1 Damasio’s Model of the Self

Damasio’s conception of a self, based upon interoception, has been extremely influential. He hypothesises a taxonomy of a ‘proto self’ - reliant on interoceptive maps - which is assembled in the brainstem and provides the organism with the feeling that its body exists (Damasio, 2010). The ‘core self’, which is created when this ‘proto-self’ is in interaction with objects, encompasses the organism’s sense of the ownership of its own body and its sense of agency. Emotion, which is coded interoceptively, is generated within the ‘core self’ during interaction with objects. The emotional salience that an organism attaches to any given object is assumed to form the basis of attentional processes. Damasio’s ‘proto self’ plus ‘core self’ is equivalent to the ‘material me’ first proposed by Sherrington (Sherrington, 1899). Damasio’s taxonomy culminates in an ‘autobiographical self’, which gives the third-person perspective, enabling humans to perceive themselves as the objects of their own thoughts (Damasio, 2010). For Damasio, the remarkable sense humans have of the invariance of the self comes about because the brain is continually engaged in re-representing the interoceptive state of the body (Damasio, 2003). According to this account, it is precisely because the body must be maintained within narrow homeostatic parameters that we have feelings of the continuity of our selves through time. This model is difficult to subject to rigorous scientific testing but has proved a powerful starting point for other theorists (Christoff, Cosmelli, Legrand, & Thompson, 2011; Panksepp & Northoff, 2009).

1.5.2 Craig’s Model of the Self, based on Interoceptive Integration

Craig’s model of ‘the sentient self’ is similarly based on interoception (Craig, 2010). Interoceptive afferent information from a wide range of sources within the body travels, by way of the thalamus, to the posterior insula cortex bilaterally, where it is represented somatotopographically and in a modality-specific manner (Björnsdotter, Löken, Olausson, Vallbo, & Wessberg, 2009; Brooks, Zambreanu, Godinez, Craig, & Tracey, 2005). According to Craig, this facilitates the re-mapping and integration, in the mid insula, of all activity related to the body, which includes the interoceptive, exteroceptive, vestibular, premotor and homeostatic systems. It is proposed that the totality of this afferent information is re-mapped into the anterior insula, where all emotional and hedonic signals arising from the body are finally integrated and become available to subjective consciousness (Craig, 2010).

There are strong similarities between Craig’s and Damasio’s models of the self. Both depend upon interoception. Both explicitly assume some form of comparator, whereby changes in the state of the self are compared from moment to moment and measured against the desired or ideal state, represented in internal body maps which are largely innate. Intriguing reports of individuals who have experienced phantom viscera provide evidence that stored body images involve interoception (Cameron, 2002, p214). Damasio suggests that consciousness is produced in ‘pulses’, while Craig refers to ‘global emotional moments’, each lasting about 125ms, which he believes make up the stream of consciousness (Craig, 2010).

A fundamental difference between Damasio’s and Craig’s models, however, is the localisation of the self. Damasio insists that the self is formed in the medial mesencephalic and diencephalic subcortical regions, (Damasio, Damasio, & Tranel, 2012; Panksepp & Northoff, 2009), only then being remapped and extended in the cortex. In defence of this argument, no cortical lesion destroys the sense of self unless it also wipes out consciousness and Damasio cites the case of a patient with bilateral lesions of insula cortex who continued to have intact, although blunted, emotions and retained his sense of self (Damasio et al., 2012; Philippi et al., 2012). Craig, by contrast, places all human self-awareness in the insula, notwithstanding the involvement of subcortical structures and the potential existence of a second pathway for interoceptive cues, involving somatosensory cortex (Couto et al., 2013; Khalsa et al., 2010).

1.6 The Insula in Interoceptive Processing

Evidence for the importance of the insula in interoception is striking. The anterior insula has broad connections across the brain and is multimodal association cortex which receives input, via the thalamus, from sensory neurons within the body (Cauda et al., 2011; Harrison, Gray, Gianaros, & Critchley, 2010; Medford & Critchley, 2010; Naqvi & Bechara, 2009; Nieuwenhuys, 2012). The modalities of this interoceptive information include temperature, itch, pain, hunger, thirst, visceral fullness, skin flushing, cramping and awareness of being ill, including nausea, (Craig, 2010). The insula is reliably activated by a diverse range of feelings, including the experience of all emotion (Craig, 2009); decision making under uncertainty (Lamm & Singer, 2010); recognition of one’s own face (Devue & Brédart, 2011); the sense of agency (Farrer et al., 2003; Sperduti, Delaveau, Fossati, & Nadel, 2011); empathy for pain (Singer, Critchley, & Preuschoff, 2009); observing and experiencing disgust (Wicker et al., 2003); olfaction (Gottfried, 2010); music (Brown, Martinez, & Parsons, 2004); and the sensual touch involved in social bonding (Björnsdotter et al., 2009). The right posterior insula is activated by the feeling of body ownership (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007; Tsakiris, 2010); by vestibular information (Lopez, Halje, & Blanke, 2008); and by estimation of elapsed time (Wittmann, Simmons, Aron, & Paulus, 2010). Moreover, attention to heartbeats activates an area of the right anterior insula (Critchley et al., 2004) that is also engaged when people rate their emotional experience. This activity correlates with the reported intensity of the emotion (Critchley & Harrison, 2013; Critchley & Nagai, 2012; Gu, Hof, Friston, & Fan, 2013; Zaki, Davis, & Ochsner, 2012).

The insula, together with the anterior cingulate cortex and medial prefrontal areas, with which it is strongly connected, are prominent elements of the set of 'cortical midline structures', which also include the temporal parietal junction and temporal pole (Northoff et al., 2006; van der Meer, Costafreda, Aleman, & David, 2010). Related to the 'default mode' of brain activity (Raichle et al., 2001), this network is activated by self-relevant tasks across a wide domain (Legrand & Ruby, 2009). Processes that activate the anterior insula can all be considered highly self-relevant. The insula's role in anxiety (Paulus & Stein, 2006), reward-related risk and uncertainty (Singer, Critchley, & Preuschoff, 2009), as well as in interoception (Craig, 2009), supports the theory that it is a cortical convergence zone that potentially plays an important role in integrating inner bodily signals with external information about the world. A number of fMRI studies also suggest that activity in the anterior insula may reflect the switching of attention between interoceptive and exteroceptive signals (Farb, Segal, & Anderson, 2012, 2013; Nagai, Critchley, Featherstone, Trimble, & Dolan, 2004). Craig has argued that the left insula is associated predominantly with parasympathetic activity, and thus with nourishment, safety, positive affect, approach behaviour and affiliative emotions, while the right insula is associated predominantly with sympathetic activity, arousal, danger, negative affect, withdrawal and emotions oriented to the survival of the individual (Craig, 2005). Alternatively there may be a degree of lateralisation of functional connectivity (Cauda et al., 2011), with the left anterior insula predominantly linked to prefrontal cortex, while the right has stronger connections to the anterior cingulate with which it is generally co-active (Medford & Critchley, 2010).

1.7 Concepts of the Self Based on Multisensory and Motor Integration

Although models of the self based on interoception are well developed, they represent only one strand of thinking (Northoff et al., 2006; Ruby & Legrand, 2007). An equally important body of research has investigated the self from a phenomenological perspective. This describes the basic, pre-conscious sense of being the 'I' of experience, thought and feelings, that resides in 'my' body (Gallagher, 2000; Zahavi, 2002), giving rise to the experience of owning 'my' body (self-identification/body ownership) and the experience of where 'I' am in space (self-location), as well as the first-person perspective (Blanke & Metzinger, 2009).

While Damasio's and Craig's models propose a self based on the integration of interoceptive cues, the phenomenological model conceives the self as a continuously recreated sensorimotor process (Ruby & Legrand, 2007), which relies on the integration of a wide range of multisensory inputs (visual, auditory, somatosensory, vestibular) together with motor signals (Aspell, Lenggenhager, & Blanke, 2012). The contribution of interoception to this integration is now being recognised (Gentsch & Synofzik, 2014; Seth, 2013). Within phenomenology a distinction is made between the sense of body ownership (the 'sensory self'), which depends principally on afferent processes, and the sense of agency (the 'acting self'), which relies on the integration of efferent motor signals with exafferent and reafferent sensory cues (Gallagher, 2000; Tsakiris & Haggard, 2005). Multisensory integration has been extensively studied with respect to body ownership (Haggard & Tsakiris, 2009; Lopez et al., 2008; Petkova & Ehrsson, 2008a; Serino et al., 2013; Tsakiris, Schütz-Bosbach, & Gallagher, 2007) and also with respect to agency (Moore, Middleton, Haggard, & Fletcher, 2012; Tsakiris & Haggard, 2005).

1.7.1 Body Ownership and Interoceptive Accuracy

The multisensory integration that underpins both body ownership and self-location (Lenggenhager, Tadi, Metzinger, & Blanke, 2007), can be studied through bodily illusions. In the rubber hand illusion, synchronous stroking a visible prosthetic hand and the participant's own hidden hand leads to the sensation of ownership of the rubber hand (Botvinick & Cohen, 1998) as well as to a perceived shift in the felt location of the real hand in the direction of the prosthesis, showing that vision has primacy in this multisensory integration. Until recently it has been assumed that the sense of body ownership in the rubber hand illusion, as well as its full body variants (Aspell, Lenggenhager, & Blanke, 2009; Ehrsson, 2007), depends on the integration of exteroceptive senses alone. However, neither vision nor touch are self-specific and some authors have suggested that it is consequently surprising that their integration is sufficient to induce body ownership illusions (Ruby & Legrand, 2007). The important contribution that interoceptive cues provide is that their input is uniquely self-specifying because the sensation they convey can only arise from within the body of the individual.

Interoception is linked to the rubber hand illusion in several ways. Firstly, the rubber hand illusion itself causes interoceptive responses. If the illusion is induced and the prosthetic hand is then threatened, this causes physiological responses (electrodermal activity) similar to those experienced when the subject's real hand is threatened (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007). This indicates that the false hand elicits emotional responses, with concomitant interoceptive signals. Heightened skin conductance responses to threats to an avatar's body have similarly been reported while subjects are experiencing the full body-swap illusion (Ehrsson, 2007). Even more strikingly, histamine reactivity increases in the 'rejected' arm during the rubber hand illusion (Barnsley et al., 2012), implying that the interoceptive system begins to disown the real hand in favour of the prosthetic and recalling Damasio's definition of 'the self' as 'whatever the immune system defines as being part of the body' (Damasio, 2003). Moreover, while an individual is experiencing the rubber hand illusion, their own hand cools down, implying that the conscious sense of the bodily self interacts with homeostatic regulation of the body (Moseley et al., 2008, but see also Sadibolova & Longo, 2014). The effect of body temperature on the rubber hand illusion operates in both directions, such that cooling the subject's real hand during stimulation leads to a stronger illusion (Kammers, Rose, & Haggard, 2011).

Moreover, individual differences in interoceptive accuracy modulate the extent to which people experience the rubber hand illusion (Tsakiris, Tajadura-Jiménez, &

Costantini, 2011). This effect has been observed both behaviourally and physiologically, through skin conductance as well as through the extent to which the skin temperature of the stimulated hand falls. It is significant only for people with below-median interoceptive accuracy, who presumably rely less on interoceptive signals of self-identification and self-location and are more likely to be subject to body ownership illusions. Similarly, during the enfacement illusion (Sforza, Bufalari, Haggard, & Aglioti, 2010), Tajadura-Jiménez and Tsakiris found that people with low interoceptive accuracy shifted their recognition of their own face more frames towards the face of a stranger when they saw that face stroked synchronously and specularly with their own (Tajadura-Jiménez & Tsakiris, 2013).

Suzuki and colleagues, using a novel ‘virtual hand’ paradigm, dispensed altogether with a prosthetic hand by filming the subject’s own hand and replaying this film to them in real time, in the location where the rubber hand would usually be placed. They showed that, if the participant’s filmed hand was made to flush slightly in synchrony with the subject’s heartbeat, then the rubber hand illusion was induced (Suzuki, Garfinkel, Critchley, & Seth, 2013). Contrary to the results of Tsakiris et al. (2011), in this paradigm it was the people with high interoceptive accuracy who experienced the greater proprioceptive drift. The important difference between these two experimental manipulations is that in the classic rubber hand illusion the interoceptive cues of the individuals with good heartbeat perception serve to anchor those participants in their own bodies and enable them to resist the illusion. However, in Suzuki et al.’s novel method, the salient interoceptive cues are now located on the real, filmed hand, predisposing people with high interoceptive accuracy to recognise it as their true body part. Similarly, causing an avatar to flash in synchrony with the participant’s own heartbeat (to enhance self-identification with the avatar’s body) facilitates performance on a task that requires participants to judge the perspective of the avatar (Aspell, Heydrich, Marillier, Lavanchy, Herbelin, & Blanke, 2013).

It has also recently been demonstrated that respiration can produce a body ownership illusion. People who saw an image of their own torso flash in synchrony with their respiration experienced a stronger sense of self-location towards the virtual body than when the flashing was asynchronous (and also when compared with an inanimate control object), although they reported no sense of ownership of the avatar (Adler, Herbelin, Similowski, & Blanke, 2014).

While the modulating influence of heartbeat perception on body ownership is now well established, there has been little investigation of the possibility that interoception provides a hitherto neglected set of self-specifying inputs to other processes that involve multisensory and motor integration.

1.7.2 Agency

A key example of such a process is the sense of agency, defined as the feeling that we are the authors of our own actions. Agency emerges in our interaction with the environment and is fundamental to models of self (Damasio, 2010; Gallagher, 2000; Seth, Suzuki, & Critchley, 2011; Synofzik, Vosgerau, & Newen, 2008b). It is well established that interoceptive accuracy modulates body ownership (Suzuki et al., 2013; Tsakiris et al., 2011) but potential influences of interoception on agency are only now being proposed, but without, as yet, direct empirical support (Gentsch & Synofzik, 2014; Seth et al., 2011). This is surprising, given that the ultimate evolutionary purpose of all action is to promote the survival and reproductive success of the organism and that this depends crucially on the maintenance of homeostatic balance (e.g. body temperature) and the pursuit of innate drives (e.g. mating), which are signalled interoceptively (Gu & Fitzgerald, 2014). The point is well demonstrated by predictive coding accounts of interoceptive processing, where homeostatic balance, signalled interoceptively (e.g. low blood sugar), can be restored either through autonomic responses (burning fat), or by movement in order (in this example) to acquire and ingest food. Interoceptive signalling and action are thus reciprocally bound, with movement being both a consequence of, and a contributor to, the maintenance of the body within the narrow range of desirable states that are compatible with life (K Friston, 2013b).

While the sense of body ownership can be produced by exafferent multisensory experience, the sense of agency depends on the integration of re-afferent sensory signals with motor cues (Haggard & Tsakiris, 2009; Moore & Fletcher, 2012). The influential comparator model emphasises the predictive aspects of this process, arguing that the sense of agency is the result of a temporal and spatial match between the predicted and the actual sensorimotor consequences of an action (Blakemore, Wolpert, & Frith, 2002). An alternative account concludes, however, that agency relies on postdictive processes, whereby we attribute an action to ourselves simply if it matches our intentions (Wegner, 2003). Synthesis of these two views is proposed in the ‘optimal cue integration’ or ‘multifactorial’ account (Moore & Fletcher, 2012; Synofzik, Vosgerau, & Voss, 2013), which suggests that predictive and postdictive cues are weighted by their relative salience and reliability. In the light of the prominence given to the sense of agency by Seth et al.’s recent model of conscious presence (Seth et al., 2011), the possibility that interoceptive/emotional cues also impact on agency is ripe for investigation (Gentsch & Synofzik, 2014).

1.7.3 Separating the Self from Other People

Theories about the origins of the self usually consider the organism as if it were surviving and acting in isolation (Sebanz, 2007). This ignores the crucial role in human evolution likely to have been played by social interaction (Knoblich & Sebanz, 2008). The discovery of mirror neurons in the premotor cortex of the macaque (Rizzolatti & Craighero, 2005) and in humans (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) gave rise to the theory that we engage our own motor cortex in order to understand and interpret the actions of others (Gallese, 2007). While mirroring of action has been the focus of the majority of research, many studies have also demonstrated the recruitment of overlapping cortical circuits during the observation and the experience of a wide range of other phenomena (Keysers & Gazzola, 2009), including pain (Lamm, Decety, & Singer, 2011), disgust (Jabbi, Bastiaansen, & Keysers, 2008; Wicker et al., 2003) and touch (Keysers et al., 2004). Such studies support the proposal that we understand the sensations and feelings, as well as the actions, of other people by analogy with the cortical representations of our own bodily sensations, emotions and actions (Gallese & Sinigaglia, 2011), which enables us to respond to the actions of others in a socially appropriate manner (Hamilton, 2013).

However, in the presence of others, individuals must be able to simultaneously represent their own precepts and actions, as well as simulating those of the other person (Sebanz, Knoblich, & Prinz, 2003). Thus, when an observer engages a state similar to that of the person observed, by activating her own representation for experiencing the observed state, she is said to experience ‘self/other overlap’ (Preston & Hofelich, 2012). The ability of people with high interoceptive accuracy to resist body ownership illusions suggests that they may be better at distinguishing ‘self’ from ‘other’, perhaps because interoceptive cues provide the necessary self-specifying input. Potentially, therefore, interoceptive accuracy may affect several outcomes that involve self/other overlap such as the ‘social Simon effect’ (Sebanz et al., 2003) and ‘automatic imitation’ (Brass, Bekkering, Wohlschläger, & Prinz, 2000).

1.8 Models of the Self Based on Free Energy

Further recent models of the self have combined the insights of earlier proposals based on interoception, with theories of the self that rely on more general multisensory integration (Apps & Tsakiris, 2013; Limanowski & Blankenburg, 2013; Quattrocki & Friston, 2014; Seth et al., 2011). These models draw on the powerful unifying framework of cortical functioning proposed by the free energy principle (Friston, 2010), together with predictive coding accounts of cortical function, to account for both ‘the sensory’ and ‘the acting self’ (Gallagher, 2000). These models take as their starting point the free energy assumption that the role of the organism is to maintain itself within a narrow range of desirable states compatible with evolutionary success (Karl Friston, 2009), for which interoception provides the vital homeostatic maps (Gu & Fitzgerald, 2014).

Seth and colleagues’ innovative, ‘interoceptive predictive coding model’ places the self, the sense of agency, conscious emotion and feelings of ‘presence’, which they define as ‘the subjective sense of reality of the world and of the self within the world’ (Seth et al., 2011), , within a predictive coding account (Karl Friston, 2009). They postulate a self based on a component for agency and another for presence. In accordance with the comparator model (Blakemore et al., 2002), within Seth et al.’s model, feelings of agency arise when the predicted sensory and motor cues from an action match the actual signals produced by moving. Presence is likewise achieved when interoceptive efference and reafference are reconciled. Importantly, although agency in this framework is assumed to rely principally on motor cues and exteroception, with presence dependent on interoception, there is vital cross-talk between these components. Sensory information from all modalities, both interoceptive and exteroceptive, must accordingly be integrated with motor cues in forming both the sense of agency and presence that go to make up the self (Seth et al., 2011).

Emotion is an integral part of Seth et al.'s model and is characterised as 'interoceptive inference'. The authors propose that conscious emotions arise when bottom-up interoceptive sensory signals are reconciled with top-down predictions about the interoceptive state of the body. Within the model, 'interoceptive predictions' about the internal state of the body depend on the integration of a wide range of inputs, incorporating the effects of exteroceptive as well as interoceptive information, plus higher-level predictions influenced, for example, by assumptions about the current social context. These cues are all integrated in a Bayes optimal fashion, according to their salience and reliability (their 'precision'). An example put forward by Pezzulo argues that the experience of night terrors may be the result of the enhanced weight accorded to interoceptive cues in the dark, when vision ceases to be reliable (Pezzulo, 2013).

In Seth et al.'s model it is assumed that interoceptive inference involves inferring the causes of changes in the perceived internal state of the body, in exactly the same way that our sensation of colour is an interpretation of wavelength-selective responses in the visual cortex (Friston, 2013a). This model is therefore related to two-stage theories of emotion, which argue that bodily percepts and emotions rely on the cognitive inferences that we draw about the internal states of our bodies (Pennebaker & Lightner, 1980; Schachter & Singer, 1962). For example, following injections of adrenalin, the emotions that people report vary depending on the experimental manipulated context (Schachter & Singer, 1962). One-stage models, by contrast, seek specific bodily signatures for the various emotions (Harrison, Gray, Gianaros, & Critchley, 2010), such as distinct patterns of cardio-respiratory activity (Rainville et al., 2006).

Complementing Seth's model, the 'free energy self' is principally concerned with self-recognition and body ownership (Apps & Tsakiris, 2013). In this model the self is continuously reconstructed as the most likely explanation for all the available sensory and motor data. In accounting for the rubber hand illusion, for example, the authors argue that, given an individual's previously learned predictions that feeling of touch and vision of touch generally co-occur, the most parsimonious explanation the brain can select, during the synchronous stroking of a fake hand and the person's hidden real hand, is that the rubber hand is truly part of their own body. By a similar set of reasoning, Limanowski and Blankenburg argue that the 'minimal phenomenological self' proposed by Metzinger (Blanke & Metzinger, 2009) is the outcome of the hierarchal generative processes involved in predictive coding. Consequently, the percept of a self is the brain's best explanation for all the available sensorimotor input (Limanowski & Blankenburg, 2013).

An important contribution of these free energy models is the proposal that the self is hierarchically distributed and underpinned by many different types of information. Signals and predictions from any modality may thus be brought to bear to resolve a conflict between cues in another, including higher-level, abstract and amodal assumptions (predictions). That the self is continually constructed through a widely distributed neural process would account for the failure to find a specific self-module in the brain

Finally, Quattrocki and Friston propose a multimodal generative model of the self, formed in early interaction with caregivers, as the emotional affordances of interoceptive states are learned by association between interoceptive cues (such as hunger) and the relevant exteroceptive signals (that provide relief). In this model, the key to separating self and other is assumed to depend on the attenuation of self-generated interoceptive cues, in order to shift attention outward onto exteroceptive cues. The authors suggest that abnormality of the oxytocin system, which they argue controls the precision of interoceptive cues, is the basis of the deficits in self-processing that characterise autism (Quattrocki & Friston, 2014). The model has yet to be subjected to rigorous testing and a number of questions remain unanswered. For example, the authors propose that theory of mind (cognitive empathy) is the result of a successful reduction in the precision (salience and reliability) of the individual's self-generated interoceptive cues, which enables the observer to avoid emotion contagion during social interaction and permits her to (cognitively) infer the interoceptive state of the other person. However, the literature on empathy (de Vignemont & Singer, 2006; Preston & de Waal, 2002; Singer & Lamm, 2009) is clear that affective empathy involves both the direct simulation of observed emotion and the simultaneous realisation that the emotion one is experiencing arises from the other person (i.e. self/other distinction). How these can be reconciled within Quattrocki and Friston's model is not immediately obvious. The model argues that self/other distinction relies on the sensory attenuation of self-generated interoceptive signals. While the difference between an exafferent and reafferent sound or touch can be clearly defined, it may be more difficult to draw this distinction in interoception, where all signals are internally generated and self-specifying.

1.8.1 Incorporating the Narrative Self into Models of the Self Based on Interoception

In neuroscience, bodily and narrative conceptualisations of the self (Damasio, 2010; Gallagher, 2000; James, 1890) have generally been treated as distinct, with the narrative self perceived as an abstract and amodal construct (Farmer & Tsakiris, 2012). However, within the free energy models of self, hierarchies, such as proto self, core self and autobiographical/narrative self (Damasio, 2010; James, 1890) represent increasing hierarchical levels (K Friston, 2011)within a single construct of the self. The nature of such a hierarchy and how it might be represented in the brain has not described but a possible model is suggested by Craig (2009). Interoceptive signals are carried on cranial nerves to the nucleus of the solitary tract, the parabrachical nucleus and hypothalamus; and by lamina 1 afferents to the thalamus (Critchley & Harrison, 2013), before being represented by numerous mappings of individual modalities in the posterior insula. They are remapped and integrated with motivationally salient exteroceptive signals, from all sensory channels, in the mid-insula, implying a posterior-to-anterior processing gradient of increasing complexity, as a hierarchy would imply. Craig proposes that further remapping of these representations in the anterior insula ultimately creates 'the material me', or bodily self. The insula's connections with limbic, prefrontal and temporal areas (Cauda et al., 2011) potentially provide the necessary further layers of the hierarchy where, for example, memories that underpin the narrative self may be integrated. This implies that the narrative self is instantiated at a higher hierarchical level than the bodily self but that the two are entirely interdependent. While interactions between interoceptive accuracy and the bodily self have been investigated in, for example body ownership, the probability that aspects of the narrative self also interact with heartbeat perception has been largely ignored.

1.9 The Motivation for this Thesis

From the review presented above, it can be concluded that interoception is fundamental to the self. Previous research has concentrated on the role of interoception in emotion and only recently has it been appreciated that interoception provides a set of uniquely self-specifying senses that make an essential contribution to the sensorimotor integration that underpins the self. The importance of interoception for the self now underpins a variety of well-developed theoretical models and has also been demonstrated by a small but growing number of empirical studies, principally in body ownership. Individual differences in interoceptive accuracy, assessed by heartbeat perception, have been successfully linked with the experience of emotion, as well as with emotional disorders, in an extensive body of research. Heartbeat perception has thus been demonstrated as an empirically valid and effective measure, despite its potential limitations. There is consequently scope to use this measure as a means to probe the role of interoception in previously neglected questions that relate to modern neurocognitive conceptualisation of the self and self/other distinction.

The aim of the six experiments presented in this thesis was, therefore, to investigate how interoceptive accuracy, measured by heartbeat perception using the Mental Tracking Method (Schandry, 1981), modulates aspects of self-processing.

A number of gaps have been identified in the literature where interoceptive accuracy may have a bearing. Conceptually the experiments fall into two groups. The first three experiments were concerned with how interoceptive accuracy interacts with attention to the self.

Heartbeat perception appears to be a trait variable, with individual differences dependent on how well people can focus their attention onto interoceptive cues. While attempts to improve heartbeat perception are generally unsuccessful, experimental manipulations that have had some effect are those that have involved enhanced attention to some exteroceptive aspect of the self. There has been some success, for example, with mirror self-observation (Weisz et al., 1988), which is generally assumed to enhance attention principally to the bodily self. However, self-recognition in a mirror involves a cognitive dimension and may equally invoke narrative, as well as bodily, aspects of self (Connors & Coltheart, 2011). Social evaluation has also been shown to improve interoceptive accuracy (Durlik, Brown, et al., 2014; Schulz et al., 2013), again suggesting that enhanced attention to narrative aspects of self can improve heartbeat perception. Importantly, free energy models of the self imply that the distinction between the bodily and narrative self is a false dichotomy. Hierarchical generative models of the self (Apps & Tsakiris, 2013; Limanowski & Blankenburg, 2013) indicate that information in any modality and at any level in the cortical hierarchy will be used to inform the ultimate precept of a self. Consequently, given that interoceptive modalities provide a set of cues that underpin the bodily self (Craig, 2010; Damasio, 2010; Seth, 2013), interoceptive signalling is likely to interact with narrative aspects of the self, at high levels of the cortical hierarchy.

The two experiments presented in Chapter 2 were, therefore, concerned with the effects of self-observation on interoceptive accuracy. Experiment 1 was based on an early report that the accidental presence of a mirror improved performance on one (but not on a second) measure of heartbeat perception (Weisz et al., 1988). By contrast with this inconclusive study, mirror self-observation was strictly controlled in Experiment 1 and a large and heterogeneous set of participants were tested. Experiment 2 built on the results of Experiment 1, to examine the effect of self-observation off line, using still self-face photographs. Experiment 2 also introduced self-relevant words, to test the potential interaction between interoceptive accuracy and narrative, as well as bodily, aspects of the self.

Phenomenological models of the self argue that the first-person perspective - the perspective from which ‘I’ perceive the world – is an element of ‘minimal selfhood’ (Blanke & Metzinger, 2009). However, an essential aspect of human self-awareness, invoked by self-focus, is perception of the ‘self as object’. This underpins the remarkable human ability to perceive oneself as the object of one’s own and other people’s perception (Duval & Wicklund, 1972). Given that interoception provides a set of senses that contribute to awareness of the body from within, Experiment 3 tested whether the tendency, in women, to prioritise awareness of their bodies from a third-person, ‘objectified’, perspective was negatively related to interoceptive accuracy.

The second strand of experiments presented in this thesis was concerned with the contribution of interoception to multisensory integration and self/other distinction. While interoceptive accuracy is known to interact with ‘the sensory self’ through body ownership (Aspell et al., 2013; Suzuki et al., 2013; Tsakiris et al., 2011), its potential impact on ‘the acting self’ (Gallagher, 2000) has previously been ignored. Three classic paradigms were used to investigate this. In Experiment 4, a ‘social Simon task’ was employed to examine whether interoceptive accuracy interacts with the tendency to represent the actions of a confederate, when performing a joint task. Experiment 5 employed a well-known test of ‘automatic imitation’, predicting that people with high interoceptive accuracy would be better able to separate self and other and would thus inhibit the tendency to imitate an observed task-irrelevant action. Experiment 6 investigated the potential contribution of interoceptive cues to the multisensory integration involved in the sense of agency, using Libet’s classic clock paradigm (Libet, Gleason, Wright, & Pearl, 1983) and taking ‘intentional binding’ (Haggard, 2005) as a measure of the sense of agency.

Most research into interoception has been within the tradition of the James-Lange theory of emotion, which treats interoceptive signals as peripheral feedback from the body (for example, as heart rate and electrodermal activity). This has tended to divert attention from the work of physiologists (Ádám, 2010; Cameron, 2002; Vaitl, 1996) which established that interoception is an additional set of senses, with its own specific sets of receptors, operating at the borders of awareness. Characterising interoception as sensory input rather than as peripheral output is potentially more useful in identifying how and where, in the course of sensorimotor integration, it is likely to impact on behaviour, cognition and feelings.

Chapter 2. The Effect of Enhanced Self-focus on Interoceptive Accuracy

2.1 General Introduction to Experiments 1 and 2

Although theoretical analyses have previously treated interoceptive and exteroceptive aspects of the self as separate sensory systems, recent research demonstrates that they interact. Body ownership illusions (Aspell, Walker, Bruno, Heydrich, & Blanke, 2013; Botvinick & Cohen, 1998; Petkova & Ehrsson, 2008) rely on the learned assumption that touch and vision-of-touch generally co-occur. However, importantly, neither vision nor touch is self-specific and it is potentially surprising that their combination is sufficient to cause these illusion (Ruby & Legrand, 2007). The interoceptive senses, conversely, provide uniquely self-specifying input because they can only originate from within the body (Ádám, 2010; Cameron, 2002; Vaitl, 1996). Potentially, therefore, the eerie phenomenology of the rubber hand illusion depends upon interoceptive processes in the autonomic nervous system (Ehrsson et al., 2007). As the illusion takes hold, histamine reactivity in the concealed hand rises (Barnsley, et al., 2012) and the skin temperature of the hidden hand falls, as if the exteroceptive stimulation was causing the autonomic nervous system to stop treating the hand as fully part of the body (Moseley, et al., 2008; but see also Sadibolova & Longo, 2014). That interoceptive and exteroceptive processes interact is further demonstrated by studies of body ownership, where people with high interoceptive accuracy are less prone to both the rubber hand illusion (Tsakiris et al., 2011) and the comparable enfacement illusion (Tajadura-Jiménez, Longo, Coleman, & Tsakiris, 2012; Tajadura-Jiménez & Tsakiris, 2013). A potential explanation is that individuals with high interoceptive accuracy have a habit of attending to their internal signals, perhaps because heartbeats and/or other interoceptive signals are innately more salient, and this heightens the self-specifying input that enables them to resist these illusions.

The motivation for the two experiments presented in this chapter was to further investigate how interoceptive and exteroceptive inputs to the self interact, by using a paradigm borrowed from social psychology. It was anticipated that heightening attention to exteroceptive aspects of the self (enhanced self-focus) might have the effect of enhancing interoceptive self-representations and thus would improve heartbeat perception. Although heartbeat perception has generally been considered a robust trait variable, two partly successful attempts to alter it potentially owe their effect to enhanced attention to the self as perceived exteroceptively, by oneself or by other people (Durlik et al., 2013; Weisz et al., 1988).

Previous unsuccessful experimental attempts to alter interoceptive accuracy have included manipulations designed to increase attention to the body. For example, a study of people with at least fifteen years intensive experience of daily meditation (designed to increase bodily self-awareness) found that the meditators were no more accurate in heartbeat perception than controls (Khalsa et al., 2008). Mindfulness training (Williams, 2010) similarly does not improve objective measures of heartbeat perception, although it boosts self-reported confidence that the participant is aware of bodily sensations (Parkin et al., 2013).

While stressors have been shown to improve interoceptive accuracy, they generally alter physiological variables that affect arousal, which is a known confound of heartbeat perception (Cameron, 2002; Jones, 1995). For example, twenty four hours of food deprivation successfully raised the Mental Tracking scores of young women (Herbert, Herbert, et al., 2012) but this manipulation is likely to have altered other affective or sensory variables, in that hunger, for example, lowers pain thresholds (Pollatos, Herbert, et al., 2012). Injections of isoprotenerol reliably raise the awareness of interoceptive sensation but as this drug elevates heart rate and general physiological arousal the results are confounded (Khalsa, Rudrauf, Sandesara, Olshansky, & Tranel, 2009). One study found that performance on the Whitehead task, surprisingly, declined for women (but not men) after a stressful Maths test (Fairclough & Goodwin, 2007) but this may be confounded by distraction. There are, however, two studies that have reported some success in temporarily changing ‘state interoceptive accuracy’. Both involved heightening attention to the self as perceived exteroceptively. The anticipation of making a public speech enhanced interoceptive accuracy measured by the Schandry method (Durlik et al., 2013) and this change was correlated with fear of negative evaluation (but see also Stevens et al., 2011). Likewise, an early experiment was partly successfully in raising heartbeat perception by the presence of a mirror (Weisz et al., 1988).

A further significant point about previously unsuccessful attempts to manipulate interoceptive accuracy is that they have generally compared changes in the mean score of the whole groups of participants between experimental conditions. They have not investigated whether the extent of change for individuals under the experimental manipulation might have been influenced by baseline individual differences in heartbeat perception (e.g. high vs. low scores). The aim of Experiments 1 and 2 was therefore to investigate whether heightening attention to exteroceptive perception of the self would impact on performance in heartbeat perception and to examine how any such effect might differ between initially good and poor heartbeat perceivers.

2.2 Experiment 1. Changes in Interoceptive Accuracy during Mirror Self-observation [1]

2.2.1 Introduction

Studies in social psychology have typically found that mirror self-observation successfully increases ‘self-focus’, which is attention to the self (Fejfar & Hoyle, 2000). Studies in this tradition have found, for example, that self-reported arousal is less influenced by experimenter suggestion when participants are exposed to a mirror (Scheier, Carver, & Gibbons, 1979). Similarly, when given mirror access, participants report fewer illusory symptoms in response to a placebo (Gibbons, Carver, & Scheier, 1979). An early study in interoception (Weisz et al., 1988) attempted to manipulate heartbeat perception using the (apparently accidental) presence of a mirror to increase self-focus, during two different heartbeat perception tasks. The results, however, were inconclusive. Participants had to tap with their index finger immediately after each heartbeat (a form of heartbeat tracking) or detect discrepancies between the rhythm of their own heartbeat and the rhythm of presented tones (a variant of the Whitehead ‘discrimination’ method). The mere presence of a mirror improved performance in the discrimination task but not in the tapping task. However, there was no control in this study for whether participants actually looked at themselves in the mirror, nor did the experiment investigate the potentially differential effects on individuals with high or low interoceptive accuracy. The heartbeat tracking method used, moreover, is no longer

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[1] This experiment was published as: Ainley, Tajadura-Jimenez, Fotopoulou, & Tsakiris. (2012). Looking into myself: Changes in interoceptive sensitivity during mirror self-observation. *Psychophysiology, 49*(11), 1672-1676.

standard because it is open to confounds created by the participant's own movement (McFarland, 1975).

Experiment 1 therefore aimed to investigate the interaction of exteroceptive and interoceptive perceptions of the self by studying the effect of mirror self-observation on accuracy in heartbeat perception. It was hypothesised that the heightened attention to exteroceptive aspects of the self involved in mirror self-observation would enhance awareness of interoceptive representation of the self and therefore improve heartbeat perception. Given that people with high interoceptive accuracy potentially perform at ceiling on heartbeat perception tasks, it was anticipated that improvement would be concentrated amongst participants with low interoceptive accuracy in the baseline, as has been demonstrated in the modulating effect of interoceptive accuracy on body ownership (Tsakiris et al., 2011). In contrast to Weisz et al. (1988), in Experiment 1 mirror self-observation was instructed and controlled and heartbeat perception was measured using the Mental Tracking Task (Schandry, 1981), which is well-validated and sensitive to individual differences (Domschke et al., 2010; Dunn et al., 2010; Ehlers et al., 1995). Self-observation versus non-self-observation were contrasted by requiring participants to look into a mirror or at a non-reflective black screen. Gender, heart rate, age, body mass index (BMI), and the participant's self-reported level of habitual exercise (as a proxy for physical fitness) were recorded as potential confounds of heartbeat perception tasks (Cameron, 2001).

2.2.2 Methods

2.2.2.1 Participants

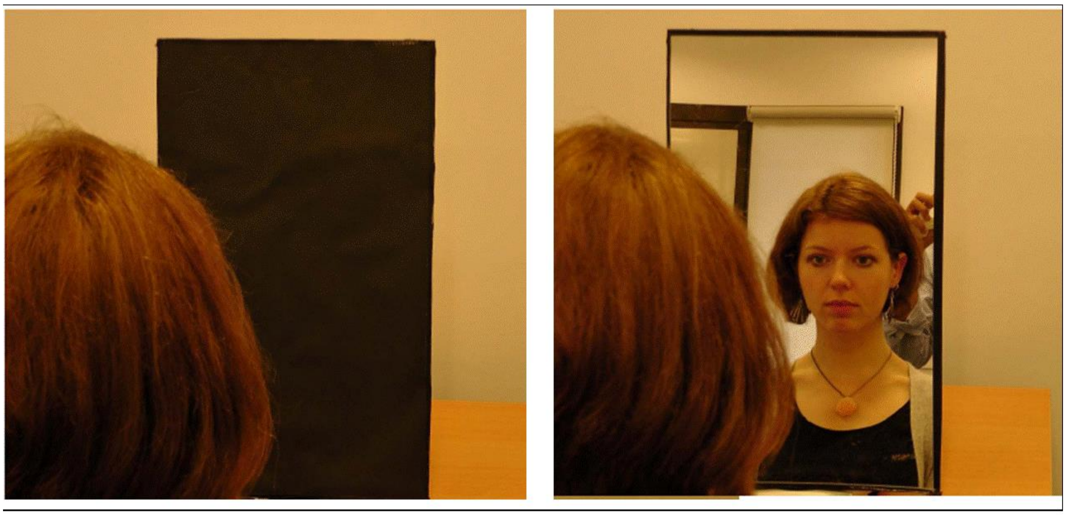
153 visitors to the 'Who am I?' Gallery at the Science Museum, London, volunteered to take part in the experiment. Data for 129 was analysed (59 male, 84 female, aged 10 to 74 years), after excluding 10 for not following the instructions and 14 for incomplete data (Table 2.1). The experiment was approved by the Department of Psychology Ethics Committee, Royal Holloway University of London. All participants gave written informed consent, were free to withdraw from the experiment at will and were debriefed after participation. Written parental consent was mandatory for all participants under 18 years of age.

2.2.2.2 Procedure

Participants typed into the computer their gender, age, height, weight and their level of habitual exercise (in hours per week). Body mass index (BMI) was calculated using the standard formula.

Interoceptive accuracy was measured twice using the Mental Tracking Method. After one training interval (15s), each condition consisted of a block of three intervals (25s, 35s and 45s) presented in random order. In the baseline condition participants were required to gaze at a black screen (30cm by 50cm) placed on an easel at eye level and at a distance of 40cm. In the mirror condition they were explicitly instructed to gaze at the reflection of their own face in a similarly sized, and positioned, mirror (Figure 2.1). The two conditions (mirror vs. blank screen) were presented in counterbalanced order.

Figure 2.1 Experimental Conditions. Left Baseline, Right Mirror Self-focus



2.2.2.3 The Mental Tracking Method of Heartbeat Perception

Participants were seated in a comfortable chair and allowed to relax for several minutes. Instructions were presented over noise-attenuating headphones. The onset and offset of each heartbeat counting trial were cued by the words ‘go’ and ‘stop’. Results are sensitive to the instructions given (Ehlers et al., 1995) so a standard instruction was used, whereby participants were asked to concentrate and try to silently count their own heartbeats, simply by ‘listening’ to their bodies, without taking their pulse. Participants were prompted at the start of each trial to keep their eyes on the screen while they were counting their heartbeats. Heartbeat signals were acquired with a piezo-electric pulse transducer, fitted to the participant's left index finger and connected to a physiological data unit (26T PowerLab, AD Instruments), sampling at 1 kHz, which recorded the derived electrical signal onto a second PC running LabChart6 software (AD Instruments). After one training interval of 15s, the three counting trials were presented in random order within each condition. No feedback was given.

2.2.2.4 Data Reduction

LabChart6 was employed to identify and count the number of R-wave peaks on the heart trace recorded for each participant in each trial, as well as to calculate the average heart rates for each trial (Jennings et al., 1981). Every heart trace was visually inspected for artefacts and the number of R-wave peaks was recounted manually if necessary. Participants were excluded where artefacts created uncertainty about the number of recorded beats. Interoceptive accuracy was calculated as {1/*3* Σ [1 - (|recorded heartbeats – counted heartbeats| /recorded heartbeats)]} (Schandry, 1981). Participants typically underestimate the number of beats. Higher scores indicate higher interoceptive accuracy.

2.2.3 Results

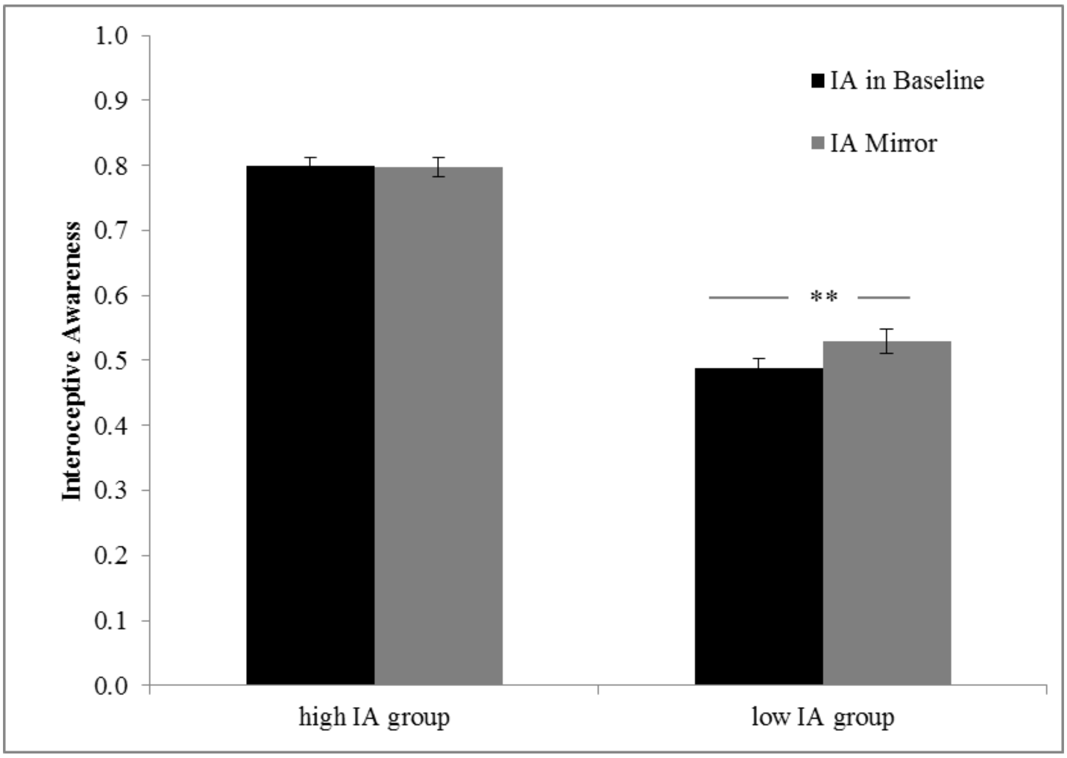
2.2.3.1 Analysis of Interoceptive Accuracy

Table 2.1 Descriptive Statistics for all Recorded Variables

	All participants (*n* = 129)	**Above median IA** (*n* = 65)	**Below median IA** (*n* = 64)
Mean interoceptive accuracy baseline (*SD*)	0.64 (*0.19*) skewness = -.35, kurtosis = -.27	0.80 *(0.10*)	0.49 (*0.13*)
Mean interoceptive accuracy mirror (*SD*)	0.66 (*0.19*) skewness = -.25, kurtosis = -.53	0.79 (*0.12*)	0.52 (*0.15*)
Mean heart rate baseline (*SD*)	75.8 (*10.5*)	72.0 (*9.7*)	79.6 (*10*)
Mean heart rate mirror (*SD*)	75.6 (*10.8*)	71.9 (*10.2*)	79.4 (*10.1*)
% Baseline performed first	52%	49%	55%
% Male	43%	48%	38%
Mean age years (*SD*)	28.7 (*13.5*)	29.6 (*13.5*)	27.8 (*13.6*)
Mean BMI (*SD*)	23.1 (*4.3*) (*n* =119)	23.6 (*4.0*) (*n* = 59)	22.5 (*4.5*) (*n* = 60)
Mean exercise hrs/wk (*SD*)	3.4 (*4.3*)	3.7 (*3.8*)	3.1 (*4.8*)

A median split analysis of the interoceptive accuracy scores (median = 0.66) was performed, in order to directly contrast performance of the groups with low and high interoceptive accuracy (IA) in the baseline (Table 2.1).

Figure 2.2 Mean Interoceptive Accuracy (IA) across Conditions for the High and Low Groups (error bars represent SEM)



***significant at the 1% level*

Data was analysed by a mixed-design ANOVA, with the experimental condition (baseline vs. mirror) as the within-subjects factor and the order of presentation of the two conditions, gender, and IA group (above vs. below median) as between-subjects factors. The change in heart rate between conditions, age, level of habitual exercise and BMI for each individual, were entered as covariates. Levene's test of equality of error variances and Box's test of equality of covariance matrices were nonsignificant. The main effect of condition (baseline vs. mirror) on interoceptive accuracy was not significant, *F*(1, 107) = 0. 02, *p* = .88. However, the interaction of experimental condition by IA group was significant, *F*(1, 107) = 6.76, *p* = .01, η^2 = 0.06, (Figure 2.1), indicating that self-observation significantly improved interoceptive accuracy for the group with below-median IA, *t*(63) = 3.46, *p* = .001, but not for the high interoceptive accuracy group, *t*(64) = 0.65, *p* = .52. There were no significant interactions between the experimental condition and gender, *F*(1, 107) = 1.67, *p* = .20; order of presentation of the two conditions, *F*(1, 107) = 0.75,

$p = .39$; change in heart rate between conditions, $F(1, 107) = 0.18$, $p = .68$; age, $F(1, 107) = 0.01$, $p = .91$; level of exercise, $F(1, 107) = 0.35$, $p = .55$; or BMI, $F(1, 107) = 0.15$, $p = .68$. The main effects of gender, $F(1, 107) = 0.30$, $p = .59$; and of order of conditions, $F(1, 107) = 3.63$, $p = .06$, were not significant. The difference between interoceptive accuracy in the mirror and in the baseline conditions correlated with interoceptive accuracy in the baseline, $r = -.30$, $p = .001$, indicating that the lower the baseline the greater the improvement in heartbeat perception in the self-focus condition. The relationship followed the equation, (IA mirror) = .11 + .85 (IA baseline). If the relationship between IA mirror and IA baseline had been non-systematic, then the slope of the regressions line would have approximated to 1, with an intercept of zero. However, the slope (.85) differed significantly from 1, $t(128) = 3.52$, indicating that IA mirror was higher for lower values of IA baseline, as also shown in the median split analysis.

2.2.3.2 Analysis of Heart Rate Data

To investigate possible differences in arousal between the baseline and mirror conditions, which would potentially confound the results, the same ANOVA design (minus the change in heart rate) was used with mean heart rate as the dependent variable. Levene's test of equality of error variances and Box's test of equality of covariance matrices were nonsignificant. The main effect of condition on heart rate was nonsignificant, $F(1, 108) = 0.11$, $p = .75$, showing that heart rates did not change significantly between the two conditions. There were no significant interactions of condition with interoceptive accuracy group, $F(1, 108) = 0.51$, $p = .48$; gender, $F(1, 108) = 0.19$, $p = .67$; order of conditions, $F(1, 108) = 0.92$, $p = .34$; exercise, $F(1, 108) = 0.06$, $p = 0.81$; BMI, $F(1, 108) = 0.10$, $p = .75$; or age, $F(1, 108) = 3.12$, $p = .08$. The main effects of gender, $F(1, 108) = 0.91$, $p = .34$, and order of conditions, $F(1, 108) = 2.30$, $p = .13$, were also both nonsignificant. As expected, a main effect of interoceptive accuracy group was observed, $F(1, 108) = 21.20$, $p < .001$, $\eta^2 = .1$ Mean heart rate was significantly lower in the high interoceptive accuracy group because heart rate was negatively correlated with interoceptive accuracy in the baseline, $r = -.28$, $p = .001$. This result has frequently been reported previously (Cameron, 2001; Fairclough & Goodwin, 2007; Knapp-Kline & Kline, 2005; Stevens et al., 2011).

2.2.4 Discussion

Interoceptive accuracy measured during mirror self-observation was compared with interoceptive accuracy in the baseline condition of looking at a black screen. Individuals with above-median interoceptive accuracy in the baseline showed no improvement while looking into a mirror but those with lower scores showed a significant improvement in interoceptive accuracy during self-observation. The effect was independent of gender, age, BMI, the order in which the conditions were presented, the participant’s habitual level of exercise and change in heart rate between the two conditions. This result contrasts with that of Weisz et al. (1988) who found a learning effect between conditions. Given that self-focus decreases available processing resources (Panayiotou & Vrana, 2004), it seems improbable that the improvement found during mirror self-observation can be explained by reduced task demands. The result is also unlikely to be attributable to higher arousal in the mirror condition (Van der Does, Van Dyk, & Spinhoven, 1997) because heart rates did not change significantly, for either group, between the two conditions.

The analysis in Experiment 1 appears to uncover an effect that was not identified in previous studies. Past research has focused on the impact of experimental treatments on the mean interoceptive accuracy of the particular populations tested, without considering the potentially different effects of the experimental manipulation on participants with high and low interoceptive accuracy. For example, attempts to enhance bodily self-focus, e.g. using a yogic breathing pattern (Fairclough & Goodwin, 2007; Khalsa et al., 2008) or a mirror (Weisz et al., 1988) reported interoceptive accuracy means for the whole group of participants but not did not examine differential effects for individuals with low or high interoceptive accuracy at baseline. In common with Weisz et al. (1988), no significant effect of the mirror vs. baseline condition was found in heartbeat tracking for the participants in Experiment 1 when taken as a whole. However, a significant effect of self-observation was demonstrated for those participants with low baseline interoceptive accuracy. The result emphasises the potential importance of low interoceptive accuracy, which has recently been recognised in clinical conditions such as eating disorders (Klabunde et al., 2013), alexithymia (Herbert et al., 2011) and depersonalisation disorder (Sedeño et al., 2014).

The experiment indicates that the exteroceptive perception of the self, when viewing one’s own face in the mirror, interacts with interoceptive representations and thus extends recent results showing that interoceptive accuracy plays an active modulatory role in weighting and integrating exteroceptive percepts relating to the body in body ownership illusions (Tsakiris et al., 2011). In this study, mirror self-observation, which relies on exteroception, enhanced low interoceptive accuracy.

Experiment 1 had a number of limitations. Participants were members of the public and were not screened for anxiety (Domschke et al., 2010) or for medical conditions such as hypertension (Koroboki et al., 2010) that are known to affect interoceptive accuracy (Cameron, 2001). No account was taken of participants’ possible use of time-estimation strategies that might have enabled them to correctly guess their heartbeats (Dunn et al., 2010; Ehlers et al., 1995). However, it is unlikely that these confounds could account for a change in heartbeat perception between conditions, as they would apply equally in both. It was not clear from Experiment 1 what aspect of the mirror image participants might (consciously or unconsciously) be depending on, for example, whether they relied on some aspect of the mirror image, such as flushing of the skin or a visible pulse (Suzuki et al., 2013). Further research was therefore required to establish whether the effect would generalise to other self-relevant stimuli.

2.2.5 Conclusion of Experiment 1

The results of Experiment 1 reinforce the proposal that the self is a complex result of interoceptive and exteroceptive representations, acting upon and reinforcing each other (Craig, 2010). In a relatively large and heterogeneous sample, they show that enhanced attention to an exteroceptive representation of the self can improve interoceptive self-representation, as indexed by the ability to perceive one’s heartbeat. Potential explanations are explored in the General Discussion. How this effect might generalise to other aspects of heightened self-focus was the subject of Experiment 2.

2.3 Experiment 2. Enhancing Interoceptive Accuracy by Heightened Attention to a Self-face Photograph and Self-relevant Words [2]

2.3.1 Introduction

In Experiment 1, the use of a mirror enhanced interoceptive accuracy in people for whom this was originally low. However, it was not known whether this effect would be restricted to live, real time, self-observation or, indeed, what other self-relevant stimuli might have a similar impact on heartbeat perception. Experiment 2 was therefore designed to clarify this question.

In the first experimental condition of Experiment 2, the use of a still photograph of the participant's face was employed, in place of a mirror image, in order to establish whether the effect in Experiment 1 depended on some aspect of the living self-image, such as a visible pulse. However, within self-focus research, 'the perceptual accuracy hypothesis' (Silvia & Gendolla, 2001) has suggested that any type of enhanced self-focused attention will improve an individual's accuracy in judging not only somatic but also cognitive aspects of the self. This strong claim potentially encompasses a wide range of potential self-relevant stimuli that could be contrasted with the enhanced attention to the body that is involved in viewing one's own face. A second experimental manipulation was therefore introduced in Experiment 2, designed to test the effect on heartbeat perception of stimuli that enhance attention to narrative aspects of the self.

Although there has been a lack of consensus on definitions and means of operationalising the self within philosophy, psychology and neuroscience (Gallagher, 2000; Neisser, 2006; Strawson, 1999), the distinction between a bodily and a narrative self, first proposed by William James, continues to structure the debate (James, 1890). The narrative or autobiographical self is defined as encompassing stored knowledge of the individual's past experience and anticipated future and has generally been treated within psychology as if it were an amodal, abstract symbolic structure (Farmer & Tsakiris, 2012; Gallagher, 2000). Damasio's

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[2] This experiment was published as: Ainley, Maister, Brokfeld, Farmer, & Tsakiris. (2013). More of myself: Manipulating interoceptive awareness by attention to bodily and narrative aspects of the self. *Consciousness and Cognition, 22*(4), 1232-1238.

taxonomy, however, proposes that the narrative self cannot be regarded as independent of the body but is instead grounded in bodily self-processes acting upon autobiographical memories (Damasio, 2010). Moreover, free energy models of the self conclude that the bodily and narrative selves are interdependent, although instantiated at different levels of the cortical hierarchy (Apps & Tsakiris, 2013). Experiment 2 therefore investigated whether the processing of self-related narrative information could bring about improvements in people's conscious awareness of their internal bodily selves, analogous to the improvements in interoceptive accuracy that were induced by the processing of physical representations of the bodily self with a mirror (Experiment 1). It also tested whether the effect of a mirror in Experiment 1 could be replicated with a still, self-face photograph.

The perceptual accuracy hypothesis suggests that any self-relevant information will improve interoceptive accuracy. However, much of the evidence for this hypothesis has been criticised on methodological grounds (Silvia & Gendolla, 2001). In a critical review of the literature Silvia and Gendolla stipulated that a valid test (for example, with regard to interoception) must compare self-reported internal perception (e.g. counted heartbeats) against an objective standard (i.e. recorded heartbeats), without introducing confounding changes in physiological variables, such as heart rate (Silvia & Gendolla, 2001).

Experiment 2 was therefore designed to fulfil these requirements, using two contrasting experimental manipulations of self-focus, with stimuli that have been frequently employed in self-focus research (Fejfar & Hoyle, 2000). The experimental condition in which participants gazed at a photograph of their own face ('the self-face condition') was compared with another in which they looked at a set of self-relevant words ('the self-relevant words condition'). As in Experiment 1, the baseline (control) condition was gazing at a blank screen. Interoceptive accuracy was measured using the Mental Tracking Task (Schandry, 1981). Gender and change in heart rate were recorded, as commonly reported confounds of cardiac awareness tasks (Knapp-Kline & Kline, 2005; Ring & Brener, 1992). Participants were students, which avoided introducing any confound of age (Khalsa, Rudrauf, & Tranel, 2009).

It was hypothesised that interoceptive accuracy would be increased by observation of the participant's own photographed face, given that recognition of one's face in a mirror and in a still photograph employs similar cortical networks (Butler, Mattingley, Cunnington, & Suddendorf, 2012). It was also anticipated that self-relevant words, which enhance attention to narrative aspects of the self, would have a similar but perhaps a smaller effect. It was expected, as in Experiment 1, that significant effects would be concentrated amongst participants who had low interoceptive accuracy in the baseline condition.

2.3.2 Methods

2.3.2.1 Participants

Participants were 45 students at Royal Holloway University of London who volunteered to take part. The data for four was excluded because of artefacts in the heart rate data. Of the remaining 41 (20 male), the mean age was 21.7 years (SD = 2.0). The experiment was approved by the Ethics Committee of the Psychology Department, Royal Holloway University of London.

2.3.2.2 Procedure

Participants gave their gender, age and height and weight. All had body mass index (BMI) within the normal range. Interoceptive accuracy was measured in three conditions.

2.3.2.3 Stimuli

A digital photograph (11cm by 13cm) was taken of the participant's face, with a neutral expression. This picture was mirror-reversed and used as the stimulus in the self-face condition. Each participant was then required to generate six self-relevant words, comprising their first name, their hometown, the school they most recently attended, their university course, the name of their best friend and the name of the most important person in their life. These words constituted the stimulus in the self-relevant words condition. They were presented in white font, arranged in a hexagonal pattern around the centre of a black computer screen, occupying the same area of screen as the self-face photograph. The stimulus for the baseline condition was a black screen with a small white fixation cross 1cm x 1cm (Figure 2.3).

Figure 2.3 Examples of Stimuli for the Three Experimental Conditions

Baseline Self-face Self-relevant words

2.3.2.4 The Mental Tracking Method of Heartbeat Perception

Interoceptive accuracy was measured using the Mental Tracking Method (Schandry, 1981), with all stimuli presented on a standard PC, as described in Experiment 1 (section 2.2.2.3). After one brief training trial (15s), there were nine trials in total, consisting of three trials in each of the three conditions – baseline, self-face and self-relevant words. The total duration of the three trials in each condition summed to 105s, with each individual trial lasting between 20s and 55s. Within these constraints, the order and duration of the nine trials was fully randomised. Heartbeat data was extracted as in Experiment 1 (section 2.2.2.4)

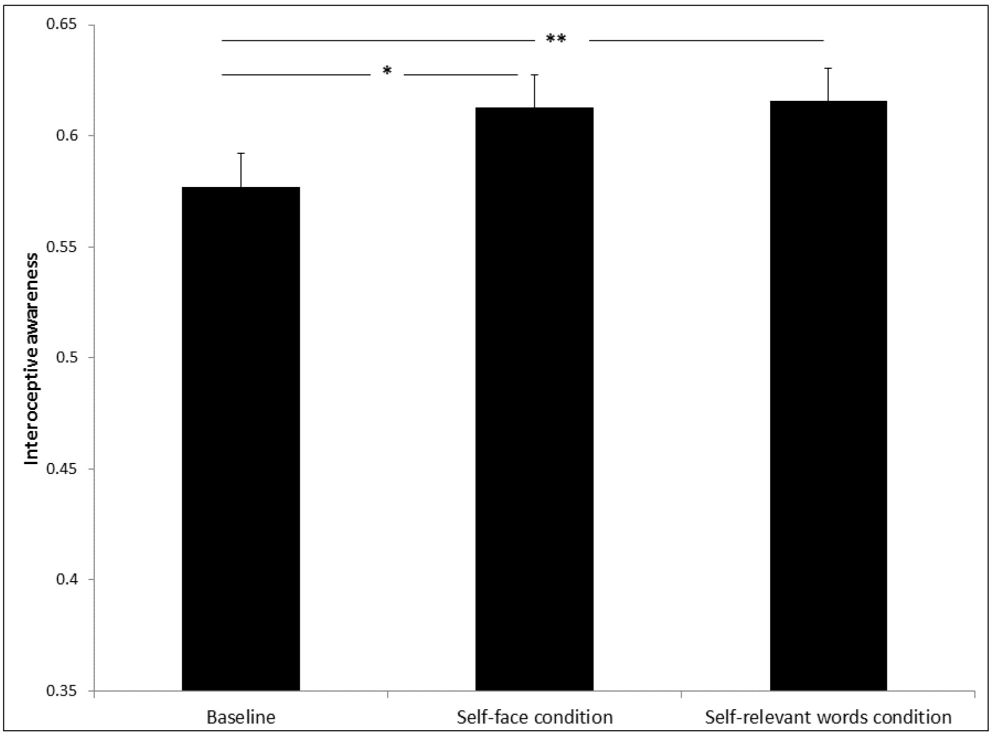
2.3.3 Results

A median split of interoceptive accuracy (IA) scores in the baseline condition (median = 0.56) was performed, to divide the participants into a high IA (above median) and a low IA (below median) group, as in Experiment 1. There were equal numbers of men and women in the two groups.

A repeated measures ANOVA was performed, with experimental condition (baseline, self-face and self-relevant words) as the within-subjects factor and with both the interoceptive accuracy group (high IA and low IA) and the participant's gender as between-subject factors. Gender effects were checked because men supposedly have higher interoceptive accuracy (Cameron, 2002). Bonferroni corrections were made for multiple comparisons. Mauchly's Test of Sphericity was nonsignificant. The main effect of gender was nonsignificant, *F*(1, 37) = 1.04, *p* = .32, and there was no interaction between gender and experimental condition, *F*(2, 74) = 0.40, *p* = .68. There was a main effect of experimental condition on interoceptive accuracy, *F*(2, 74) = 5.58, *p* = .01, η^2 = .13 (Figure 2.2). Paired sample *t* tests showed that both experimental manipulations significantly improved interoceptive accuracy, compared with the baseline; for the self-face condition, *t*(40) = 2.51, *p* = .02, and for the self-relevant words, *t*(40) = 2.77, *p* = .01. The difference in interoceptive accuracy between the self-face and the self-relevant words conditions was nonsignificant, *t*(40) = 0.26, *p* = .79.

Finally, the interaction of interoceptive accuracy group and experimental condition was nonsignificant, *F*(2, 74) = 0.63, *p* = .54. Thus, overall, the results show that both manipulations of self-focus resulted in improved interoceptive accuracy and that this improvement was independent of the participant's baseline interoceptive accuracy.

Figure 2.4 Interoceptive Accuracy in Each of the Three Experimental Conditions (error bars represent SEM)



***significant at the 1% level* **significant at the 5% level*

To test whether the effects of the experimental manipulation on interoceptive accuracy were influenced by differences in levels of arousal between the three conditions, the ANOVA analysis was repeated using heart rate as the dependent variable. The three conditions were the within-subjects factor. Interoceptive accuracy group and participant's gender were the two between-subjects factors. Mauchly's Test of Sphericity was nonsignificant. There was no main effect of experimental condition on heart rate, $F(2, 74) = 2.10$, $p = .13$. The main effect of gender was nonsignificant, $F(1, 37) = 0.81$, $p = .38$, and there was no interaction of gender with experimental condition, $F(2, 74) = 1.61$, $p = .21$. There was no interaction of experimental condition and interoceptive accuracy group, $F(2, 74) = 2.94$, $p = .06$. However, there was a significant main effect of interoceptive accuracy group on heart rate, $F(1, 37) = 6.86$, $p = .01$, $\eta^2 = .16$, because, as frequently reported in the literature, individuals with low interoceptive accuracy generally have slower heart rates (Cameron, 2001; Fairclough & Goodwin, 2007; Knapp-Kline & Kline, 2005; Stevens et al., 2011). This main effect did not interact with the experimental conditions, which therefore rules out the possibility that the observed changes in interoceptive accuracy can be accounted for by individual differences in average heart rate/arousal. Change in heart rate and change in interoceptive accuracy were not correlated, either between the self-face condition and baseline, $r = -.06$, $p = .70$, or between the self-relevant words condition and the baseline, $r = -.16$, $p = .33$.

Because the median in Experiment 2 was relatively low (.56), participants were also divided into two alternative groups depending on whether their interoceptive accuracy was above or below .66, which was the median reported in Experiment 1. There was a significant effect of both self-focus conditions only in the group with interoceptive accuracy less than .66, ($n = 28$). In this lower-IA group, paired samples t tests showed that the difference between interoceptive accuracy in the self-face and baseline conditions was significant, $t(27) = 2.08$, $p = .045$. The difference between interoceptive accuracy in the self-relevant words condition and in baseline was also significant $t(27) = 2.18$, $p = .04$. In the higher-IA group (IA > .66) the results were not significant, $t(12) = 1.36$, $p = .20$, for self-face vs. baseline, nor for self-relevant words vs. baseline, $t(12) = 1.64$, $p = .13$. However, the small number of participants (*n* = 13) in the group with IA > .66 renders these latter figures unreliable.

2.3.4 Discussion

Attention to the self was heightened in Experiment 2, using two manipulations which are employed in self-focus research. In the self-face condition participants looked at a still photograph of their own face and in the self-relevant words condition they gazed at self-generated, autobiographical words. The effect of these two manipulations on interoceptive accuracy was measured using the Mental Tracking Method of heartbeat perception (Schandry, 1981). Interoceptive accuracy was significantly enhanced in both of these heightened self-awareness conditions, compared to the baseline of looking at a blank screen. These findings extend those of Experiment 1, which showed that mirror self-observation significantly improved heartbeat perception for participants with below-median interoceptive accuracy in the baseline. Experiment 2 indicated that improvement in interoceptive accuracy is elicited by a still, self-face photograph and similarly by attention to the narrative aspects of the self, such as one’s own name or the names of significant others. Experiment 2 therefore adds to converging evidence that interoception interacts with representations of the self as perceived exteroceptively (Maister & Tsakiris, 2014; Tsakiris et al., 2011).

It had been anticipated in Experiment 2 that improvements in heartbeat perception during heightened self-focus would be confined to the below-median interoceptive accuracy group (as in Experiment 1, where median interoceptive accuracy was .66, as well as in Maister and Tsakiris (2014) where the median was .64). In Experiment 2, however, whether the participants had above or below-median interoceptive accuracy made no significant difference to the effect of the experimental manipulations. This may be explained by the relatively low mean and median interoceptive accuracy scores recorded in Experiment 2, which can be attributed to normal sampling variation. Task instructions (Ehlers et al., 1995) and experimental paradigm were similar in all three of these studies. Means as low as .5 (Sütterlin et al., 2013) and as high as .84 (Werner et al., 2010) have been reported for samples of participants tested using the Mental Tracking Method. In Experiment 1, the relatively large (*n* = 129) and heterogeneous sample (aged 10-74yrs) would account for median interoceptive accuracy close to middle of the published range.

In Experiment 1 the effect of mirror self-observation on interoceptive accuracy was open to the potential confound that participants might have been using some aspect of their own reflection, such as a visible pulse, to improve their heartbeat perception. Experiment 2 shows that the result does not depend on a living, moving image or on facial expression, because participants viewed static pictures of their face. Morever, the changes in interoceptive accuracy in Experiment 2 cannot be the result of learning effects, or of regression to the mean, because the nine trials were fully randomised, such that a trial in any one experimental condition was followed by another that was likely to be in a different condition.

A potential limitation of Experiment 2, however, is that it does not directly establish whether the effect in the self-face condition depends of looking at one’s own face or could be achieved by gazing at any face. However, Maister and Tsakiris, compared a self-face photograph condition (identical to that of Experiment 2) with another in which participants gazed at a similar photograph of a stranger, matched for age and gender. Heartbeat perception improved (for individuals who had below-median interoceptive accuracy in the baseline condition) only when participants looked at their own faces (Maister & Tsakiris, 2014).

Enhanced self-focus has been reported to increase arousal (Denson, Creswell, & Granville-Smith, 2012) which, in turn, may improve heartbeat perception (Van der Does et al., 1997). This is unlikely to have been the cause of the increased interoceptive accuracy observed in Experiment 2, because average heart rate did not change significantly between conditions. Moreover, in neither of the heightened self-focus conditions was the improvement in interoceptive accuracy correlated with resting heart rate or with change in heart rate. Self-focus is known to decrease available processing resources (Panayiotou & Vrana, 2004), so the improvements observed in heartbeat perception during heightened self-focus cannot be explained by reduced task demands.

A potential confound is that the complexity of the stimuli in Experiment 2 differed between the three conditions. In his ‘competition of cues’ hypothesis, Pennebaker (1980) argued that additional demands on exteroceptive perception reduces participants’ ability to concentrate on their interoceptive sensations. It might therefore be expected that interoceptive accuracy would fall in both the enhanced self-focus conditions, which involve more cognitive load than the baseline. Maister and Tsakiris, however, showed that looking at a self-photograph raised the interoceptive accuracy of participants with below-median interoceptive accuracy in the baseline, whereas similar attention to the face of a stranger did not (Maister & Tsakiris, 2014). Their two experimental conditions were very similar in cognitive load and processing demands, differing only in self-focus. This reinforces the conclusions that the changes detected in Experiment 2 depend on increased self-focus rather than differences in stimulus complexity. Moreover, Maister and Tsakiris found no change in interoceptive accuracy, between the baseline and stranger’s face condition, which indicates that differences in complexity of the stimuli cannot account for the changes in interoceptive accuracy observed in the Experiment 2.

Further limitations of Experiment 2 are similar to those of Experiment 1. Participants were not screened for anxiety (Domschke et al., 2010) or for clinical conditions that may impact on interoceptive accuracy. No allowance was made for the potential use of time-estimation strategies (Dunn, Galton, et al., 2010). However, these confounds would apply equally in each of the three experimental conditions and are therefore unlikely to account for the improvements observed between the two heightened self-focus conditions and the baseline.

2.3.5 Conclusion of Experiment 2

The results of Experiment 2 show that enhanced attention to the self as perceived exteroceptively (through vision of one’s own face or self-relevant words) enhances perception of internal interoceptive processes. Both experimental manipulations were equally successful, although they act at different levels of the hierarchical representation of the self. This demonstrates that aspects of the bodily and narrative self are interdependent because enhanced attention to either has similar effects in improving the accuracy of internal perception – a result that is in accordance with predictive coding accounts of the self (Apps & Tsakiris, 2013) and provides support for the perceptual accuracy hypothesis (Silvia & Gendolla, 2001).

2.4 General Discussion of Experiments 1 and 2

Experiments 1 and 2 add to a growing literature indicating that interoceptive and exteroceptive perception interact in forming the sense of self and the results are consistent with the proposal that individual differences in interoceptive accuracy reflect differences in the tendency to attend to interoceptive cues.

The results can be explained in terms of free energy models of the self and, behaviourally, by the perceptual accuracy hypothesis. Potentially the most important aspect of the results of Experiments 1 and 2 is that they provide support for models proposing that the self is distributed across multiple hierachical layers of the brain, such that incoming information, in any modality and at any level of the hierarchy, will prime self-representations at all other levels (Apps & Tsakiris, 2013). This implies that the traditional distinction between a bodily self and an amodal, narrative self is essentially false (Farmer & Tsakiris, 2012). Experiment 1 showed that attention of a bodily aspect of the self (the mirror image) enhanced the accuracy of participants' interoceptive self-representations (in people for whom this was low). Experiment 2 expanded on this, showing that although cues that enhance attention to the bodily and narrative selves act at different levels of the cortical hierarchy that instantiates the self, they have similar effects in enhancing attention to interoceptive representation. These temporarily reach awareness, boosting the heartbeat perception of people with low trait interoceptive accuracy, while people with high interoceptive accuracy are presumably already at ceiling.

Behaviourally, the results of Experiments 1 and 2 provide support for the 'perceptual accuracy hypothesis' (Silvia & Gendolla, 2001), which proposes that any type of enhanced self-focus will improve the accuracy of self-perception. Previous evidence suggesting that increased self-focus enhances interoceptive accuracy has been marred by methodological issues. In their 'sceptical review' of the literature on interoception and self-focus, Silvia and Gendolla point out that most published studies have relied on questionnaire measures of trait self-focus and on self-reported interoceptive sensations. Many have also failed control for arousal (for example they have used exercise or caffeine as experimental manipulations). This necessarily undermines any conclusions that can be drawn from previous research. The design of Experiments 1 and 2 meets these objections by fulfilling the conditions that Silvia and Gendolla stipulate for an adequate test of the perceptual accuracy hypothesis (Silvia & Gendolla, 2001). They recommend the use of an objective physiological test for the awareness of interoceptive sensation and require that changes in potential confounding variables, such as arousal, be ruled out. Furthermore, Experiments 1 and 2 used within-participants designs and experimental manipulations of self-focus, whereas many previous studies have relied on self-report psychometric measures to identify groups of people with low and high trait self-awareness. Silvia and Gendolla also proposed that ‘consistency seeking’ could account for the result of many flawed studies that have previously been used to support the perceptual accuracy hypothesis (Silvia & Gendolla, 2001). When attention is focused on the self, people are motivated to make consistent judgments and to meet task standards. Consistency seeking is particularly likely where participants are aware of a standard that they are expected to meet. In both Experiments 1 and 2 there was no apparent standard and no feedback and the task was of similar difficulty in each condition. Consistency seeking would have tended to remove differences in interoceptive accuracy across the various experimental conditions and cannot account for the findings.

The mechanism that is assumed to drive the perceptual accuracy hypothesis depends on the effects of directing attention inward. The results of Experiments 1 and 2 therefore are in accord with the proposal that interoceptive accuracy reflects an individual’s ability to attend to internally. Pennebaker, in his ‘competition of cues hypothesis’, proposed that the ability to accurately detect internal bodily signals is proportional to the amount of available ‘internal information’ and is therefore inversely related to the presence of competing ‘external information’ (Pennebaker, 1982). It follows that more accurate self-perception reflects the ability to concentrate on internal cues, while disregarding distracting external information. In Experiments 1 and 2 the self-focus manipulations can be assumed to have enhanced the accuracy of self-perception by shifting attention from the external environment to internal aspects of self-processing. A probable explanation is that people with high interoceptive accuracy already have an innately stronger tendency to attend to internal cues, compared to individuals with low interoceptive accuracy. The latter would therefore be likely to benefit more from these experimental manipulations.

Chapter 3: Interoceptive Accuracy and the 'Self as Object'

3.1 Experiment 3. Interoceptive Accuracy and Self-objectification in Young Women [3]

3.1.1 Introduction

Self-awareness from a first-person perspective, as the lived experience of the body, is assumed to be based on interoception (Craig, 2010; Damasio, 2010). However, humans also have the remarkable ability to consider themselves from a third-person perspective, as if they were spectators standing outside themselves, adopting an exteroceptive representation of the body and experiencing themselves as the objects of their own thoughts (Blanke & Metzinger, 2009; Keenan, Wheeler, Gallup, & Pascal-Leone, 2000; Rochat & Zahavi, 2011).

A notable aspect of the improvements in interoceptive accuracy observed in Experiments 1 and 2 is that they relied on temporarily heightening participants' awareness of their bodies as the objects of their own perception and thought. A related finding, from the psychology of women, is that those individuals who are generally preoccupied with how their bodies appear from such a third-person perspective are vulnerable to a number of mental health conditions, including eating disorders, depression and sexual dysfunction (Moradi & Huang, 2008). Furthermore, sufferers from anorexia nervosa, which is associated with a distorted sense of the body as seen from a third-person perspective (Garner, Garfinkel, Stancer, & Moldofsky, 1976), have lower interoceptive accuracy than controls (Klabunde et al., 2013; Pollatos et al., 2008). Likewise, psychosomatic complaints have been associated with low awareness of interoceptive sensations (Mussgay et al., 1999). The blunted autonomic reactivity reported in such patients suggests that inaccuracy in the perception of interoceptive signals may underlie their condition (Pollatos et al., 2011).

Taken together, studies of the interaction between the body perceived interoceptively and exteroceptively suggest that the degree to which people are aware of internal sensory states (i.e. their trait interoceptive accuracy) may be

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[3] This experiment was published as: Ainley & Tsakiris. (2013). Body conscious? Interoceptive awareness, measured by heartbeat perception, is negatively correlated with self-objectification. *PloS One*, *8*(2), e5568.

related to their sensory perception of their bodies from a third-person perspective. Experiment 3 aimed to investigate this.

Neurocognitive research has considered awareness of self in terms of interoception (Craig, 2009; Critchley et al., 2004). Within social psychology, by contrast, self-awareness is generally assessed by self-report. The purpose of Experiment 3 was to compare measures of self-awareness from within these two traditions, specifically to assess the relationship of interoceptive accuracy to several instruments that purport to measure an individual’s preoccupation with the self as perceived exteroceptively.

In social psychology, self-awareness has been studied as ‘objective self-focus’, which was developed as part of a model of self-regulation and affect (Duval & Wicklund, 1972) whereby, when the individual's attention is focused inward, the self becomes the object of its own thoughts and perceptions (Silvia & Gendolla, 2001). An important assumption of this model is that people compare the self they perceive against some salient ideal and then attempt to reduce the discrepancy between the two (Carver & Scheier, 1998). Self-focus is therefore thought to be inherently aversive because the real and desired self are seldom perfectly congruent. Theories of self-focus distinguish between ‘private self-consciousness’, which is the tendency to reflect continually on inner thoughts, sensation and feelings, and ‘public self-consciousness’, in which the individual is concerned with how his/her self is perceived by others (Carver & Scheier, 1998). The most commonly used self-report measure of self-focus is the Self-Consciousness Scale (Fenigstein et al., 1975).

Within the self-focus tradition, Fredrickson and Roberts proposed ‘objectification theory’ (Fredrickson & Roberts, 1997). They hypothesised that cultural attitudes that treat women’s bodies as objects for men’s gratification predispose women to value their bodies in terms of physical attractiveness, while men by contrast esteem their own bodies for physical effectiveness. Women may come to internalise this objectification and consequently adopt an observer’s perspective as the primary view of their physical selves. This ‘self-objectification’ is proposed as an important causal factor in women’s mental ill-health, leading to body shame, anxiety and eating disorders, as well as being a potential precursor to depression and sexual dysfunction (Fredrickson & Roberts, 1997).

Women who ‘self-objectify’ persistently attend to and monitor the outward appearance of their bodies. Given that interoceptive accuracy measures the tendency to attend to internal signals and potentially indexes the strength of interoceptive self-representations, an inverse relationship between self-objectification and interoceptive accuracy is predicted by the objectification literature. It has frequently (though not invariably) been reported that interoceptive accuracy is lower in women than in men (Blascovich et al., 1992; Harver et al., 1993; Jones, 1995). The inferior performance of women has previously been studied in terms of known physiological confounds of interoceptive accuracy, such as women’s higher body fat, their generally lower physical fitness and differing cardiovascular variables, including smaller stroke volume of the heart (Cameron, 2001; Jones, 1995). Fredrickson and Roberts, however, proposed instead that the reported gender difference in interoceptive accuracy is a direct result of self-objectification, which focuses attentional resources on the body as perceived from the outside, at the expense of the relative insensitivity of women to their own internal bodily cues. It appears that this strikingly novel prediction has never been tested within heartbeat perception research. The principal aim of Experiment 3 was therefore to investigate this, as an aspect of the interaction of interoceptive and exteroceptive aspects of the self.

To measure trait self-objectification, Fredrickson and colleagues developed the Self-objectification Questionnaire (Fredrickson, Roberts, Noll, Quinn, & Twenge, 1998). They originally operationalised state self-objectification by requiring participants to wear either a swimsuit (high state objectification) or a loose sweater (low state objectification). Participants in the swimsuit condition were observed to eat smaller amounts of the cookies that they were invited to sample during the experiment (Fredrickson et al., 1998). The authors argued that further research would find links between self-objectification and eating disorders, mediated either by body shame (McKinley & Hyde, 1996) or by a lack of attention to ‘internal bodily states’ (in other words, low interoceptive accuracy). A number of studies have confirmed the first part of this hypothesis, establishing that the relationship is mediating by body shame (Moradi & Huang, 2008). In self-objectification research, however, finding valid and reliable measures for the ‘awareness of internal bodily states’ has proved problematic. The Body Consciousness Questionnaire (Miller, Murphy, & Buss, 1981) and in particular its Private Body Consciousness subscale, has been widely used as a measure of inner bodily awareness in this field. However, a review of the objectification literature (Moradi & Huang, 2008) found little evidence for its role in mediating between self-objectification and cognition, eating disorders, negative affect or depression (Szymanski & Henning, 2006; Tiggemann & Kuring, 2004; Tiggemann & Slater, 2001). Some authors have concluded that internal body awareness has been widely mismeasured and misconceptualised in the objectification literature (Myers & Crowther, 2008). A review of commonly used body awareness questionnaires underlines this lack of consensus on how body awareness should be assessed (Mehling et al., 2009).

A further motivation for Experiment 3 was that surprisingly few studies in objectification research have attempted to employ non-questionnaire-based measures of body awareness, such as behavioural or neurophysiological measures. A notable exception is an experiment by Eshkevari and colleagues who used the rubber hand illusion as a psychophysiological measure of body awareness (Eshkevari, Rieger, Longo, Haggard, & Treasure, 2011). Scores on the Self-objectification Questionnaire significantly predicted the extent to which participants experienced this illusion and thus the potential malleability of their sense of bodily self. Individuals who are susceptible to the rubber hand illusion (Botvinick & Cohen, 1998) are also more likely to have eating disorders (Mussap & Salton, 2006), suggesting a possible link from self-objectification to disordered eating, through the mediating effect of body awareness, as measured by the rubber hand illusion. Given the importance of body awareness to self-objectification research and the mixed results obtained with various questionnaire measures, it is surprising that heartbeat perception has not been tested as a measure of internal body awareness within self-objectification research.

Experiment 3 was intended to remedy this deficiency, by studying the links between interoceptive accuracy and those commonly used self-report measures that are designed to assess awareness of the body, as perceived exteroceptively and/or interoceptively. Participants were young women, so as to avoid introducing other confounding gender effects. Interoceptive accuracy was measured using the Mental Tracking Method and compared with the participants' scores on the Self-objectification Questionnaire (Fredrickson et al., 1998), the Self-consciousness Scale (Fenigstein et al., 1975) and the Body Consciousness Questionnaire (Miller, Murphy, & Buss, 1981).

The principal hypothesis was that self-objectification would be linked to interoceptive accuracy, reinforcing the results of Experiments 1 and 2 which found interaction between interoceptive and exteroceptive aspects of the self. It was expected that the relationship would be negative, such that a tendency to attend to the body as perceived interoceptively (high interoceptive accuracy) would effectively inhibit excessive attention to exteroceptive aspects of the self (high self-objectification). It was similarly anticipated that scores on the Public Self-consciousness and Public Body Consciousness scales would interact with interoceptive accuracy and potentially with Self-objectification scores. Both these scales, which are frequently used in self-focus research, refer to the self as perceived from a third-person perceptive and have apparent similarities to self-objectification (Miner-Rubino, Twenge, & Fredrickson, 2002). Although Frederickson and Robert proposed that lower interoceptive accuracy in women is a result of self-objectification, it was hypothesised in this experiment that interoceptive accuracy would predict Self-objectification scores, because the former is a trait variable, while the latter is supposedly acquired by enculturation.

A final aim in Experiment 3 was to test whether Private Body Consciousness correlates with interoceptive accuracy because Private Body Consciousness is frequently proposed as a measure of the tendency to attend inwardly (Wheeler et al., 2008). Miller and colleagues, for example, found that both men and women high in Private Body Consciousness reported more bodily changes when they were secretly given caffeine, compared to those who were low in Private Body Consciousness and also compared to participants who were high in Private Body Consciousness but had received a placebo (Miller et al., 1981). Their findings imply that Private Body Consciousness is a good indicator of interoceptive accuracy. Consequently, this scale has frequently been used as a measure of body awareness in the self-objectification literature but with very limited success (Muehlenkamp & Saris-Baglama, 2002; Szymanski & Henning, 2006; Tiggemann & Kuring, 2004; Tiggemann & Slater, 2001).

3.2.2 Method

3.2.2.1 Participants

Participants were 50 female students at Royal Holloway University of London, who volunteered to take part. They were aged 19-26 years, (mean = 21.0 years, SD = 1.3). Three participants were excluded for artefacts on their heartbeat traces and one for failing to comply with the instructions on the Self-objectification Questionnaire. The experiment was approved by the Ethics Committee of the Psychology Department, Royal Holloway University of London.

3.2.2.2 Procedure

Participants reported their gender, age, height and weight. All had body mass index (BMI) within the normal range. Interoceptive accuracy was measured using the Mental Tracking Method, as described in Experiment 2 (section 2.2.2.3). There were three trial intervals, fully counterbalanced and always summing to 105s, which were selected from a set of intervals ranging from 20s to 55s. Interoceptive accuracy was calculated as described in section 2.2.2.4. Participants then completed the Self-objectification Questionnaire, the Self-consciousness Scale and the Body Consciousness Questionnaire.

3.2.2.3 Questionnaires

The Self-objectification Questionnaire (SOQ)

The Self-objectification Questionnaire (Fredrickson et al., 1998) measures the extent to which individuals view their bodies in observable, appearance-based (i.e. objectified) terms, versus non-observable competence-based terms. Participants are required to rank ten body attributes by how important each is to their own physical self-concept, from 0 (for least impact) to 9 (greatest impact). Self-objectification scores are calculated by subtracting the summed ranks given to the five competence-based attributes (e.g., health, or energy) from the summed ranks of the five appearance-based attributes (e.g., physical attractiveness, or body measurements). Scores range from -25 to +25, with higher scores indicating greater emphasis on appearance, which is interpreted as greater self-objectification. The SOQ has good test-retest reliability (.92, cited in Miner-Rubino et al., 2002).

The Self-consciousness Scale (SCS)

The Self-consciousness Scale (Fenigstein et al., 1975) consists of three subscales, designed to measure self-focused attention. The Private Self-consciousness subscale is made up of ten items to assess the extent to which individuals focus on internal thought, sensations and feelings (e.g. 'I'm always trying to figure myself out'). Public Self-consciousness is measured by seven questions referring to focusing on oneself as an object of an observer's scrutiny (e.g. 'I usually worry about making a good impression'). There are six questions on the Social Anxiety subscale, which measures distress caused by interacting with other people (e.g. 'I have trouble working when someone is watching me'). Participants respond on a 5-point Likert scale, ranging from 0 (extremely uncharacteristic of me) to 4 (extremely characteristic). Higher scores indicate greater self-consciousness/social anxiety. The three sub-scales appear to be relatively independent (Fenigstein et al., 1975). The SCS has fairly good reliability, with Cronbach's alpha ranging from .73 to .84 (Mor & Winquist, 2002).

The Body Consciousness Questionnaire (BCQ)

The Body-Consciousness Questionnaire (Miller et al., 1981) extends the concept of self-consciousness to awareness of the body. There are three subscales, which are Public Body Consciousness, Private Body Consciousness and Body Competence. The Private Body Consciousness subscale consists of five items designed to measure the tendency to focus on internal body sensations (e.g. 'I am sensitive to internal body tensions'). Public Body Consciousness contains six questions to assess consciousness of the body as perceived by an observer (e.g. 'I am very aware of my best and worst facial features'). Body Competence includes five items, which measure the individual's sense of body effectiveness. These Body Competence questions are somewhat similar to the competence-based questions in the Self-objectification Questionnaire (e.g. 'I'm better coordinated than most people'). Participants respond on a 5-point Likert scale, ranging from 0 (extremely uncharacteristic) to 4 (extremely characteristic). Higher scores represent greater body awareness/body competence. In a review of body awareness measures, the BCQ had high reliability and validity compared with other scales (Mehling et al., 2009).

3.2.3 Results

Recorded values of the mean and standard deviation (SD) for all measures were similar to the values previously published by the authors of the various scales (Table 3.1). Distributions for all measures were close to Gaussian, fulfilling an essential precondition for the use of multiple regression. In addition to using Private Self-consciousness as a single measure, it was split it into subscales of Self-reflectiveness and Internal State Awareness (Anderson, Bohon, & Berrigan, 1996).

Table 3.1 Descriptive Statistics for IA and all Self-report Measures

	Min	Max	Mean	SD	Skewness	Kurtosis
Interoceptive Accuracy	.22	.85	.59	.16	-.40	-.24
Self-objectification	-25	25	-1.65 [c]*1.09*	13.80 [c]*14.42*	.39	-.66
Private Self-consciousness	14	36	24.83 [a]*26.6*	4.79 [a]*5.1*	-.12	-.10
Public Self-consciousness	10	27	19.09 [a]*19.3*	3.75 [a]*4.0*	-.01	-.26
Social Anxiety	4	23	13.04 [a]*12.8*	4.57 [a]*4.5*	.01	-.38
Private Body Consciousness	8	19	12.7 [b]*12.0*	2.56 [b]*3.3*	.02	-.29
Public Body Consciousness	9	22	16.41 [b]*17.1*	3.0 [b]*3.3*	-.02	-.25
Body Competence	3	14	8.78 [b]*10.0*	2.56 [b]*2.5*	-.16	-.52

[a] *Mean published values, n = 253 (Fenigstein et al., 1975)*

[b] *Mean published values, n = 353 (Miller et al., 1981)*

[c] *Mean published values, n = 421 (Miller et al., 1981)*

There were significant inter-correlations amongst several of the measures used (Table 3.2). With two exceptions these were close to the inter-correlations previously reported by the authors of the various scales. However, unlike Miller and colleagues, in this group of participants no significant correlation was found between Public Self-consciousness and Private Body Consciousness, nor between Private Self-consciousness and Body Competence (Miller et al., 1981).

It had been hypothesised that Self-objectification scores would be predicted by interoceptive accuracy together with Public Self-consciousness and Public Body Consciousness. Multiple regression (entry method), with Self-objectification as the dependent variable and all other measures entered as independent variables, showed that interoceptive accuracy, Public Body Consciousness, and Private Body Consciousness together explained 31% of the variance in the self-objectification scores (Table 3.3). Neither Public Self-consciousness, nor any of the other questionnaire measures, made any significant contribution as a predictor. BMI and the interaction of BMI with all three significant regressors added nothing to the explanatory power of the model. The three significant predictors were not inter-correlated (Table 3.2), indicating an absence of multicollinearity within the model. No outlier analysis was performed.

Table 3.2. Correlations between the Measures

		Self-Objectification Questionnaire	IA	Private SCS	Public SCS	Social Anxiety	Private BCQ	Public BCQ	BC
Interoceptive Accuracy (IA)	Correl.	-.31*							
	Sig.	.03							
Private Self-consciousness	Correl.	.17	-.29						
	Sig.	.26	.05						
Public Self-consciousness	Correl.	.28	-.24	.36*					
	Sig.	.06	.11	.01					
	Published correl.			[b]*.23***					
Social Anxiety	Correl.	.26	-.26	.10	.30*				
	Sig.	.08	.09	.53	.04				
	Published correl.			[b]*.11*	[b]*.21***				
Private Body consciousness	Correl.	-.18	-.04	.31*	-.08	-.24			
	Sig.	.23	.80	.04	.60	.10			
	Published correl.			[a]*.45***	[a]*.28***	[a]*.12*			
Public Body consciousness	Correl.	.47**	-.07	.28	.59**	.08	.09		
	Sig.	<.001	.63	.06	<.001	.59	.55		
	Published correl.			[a]*.33***	[a]*.66***	[a]*.12*	[c]*.37*		
Body Competence (BC)	Correl.	-.14	.37*	<.001	-.15	-.45**	-.35*	.05	
	Sig.	.36	.01	.98	.32	<.001	.02	.72	
	Published correl.			[a]*.31***	[a]*.09*	[a] *-.20*	[c]*.21*	[c]*.21*	
[d] Self reflectiveness	Correl.	.17	-.28		.36*	.21	.25	.30*	-.13
	Sig.	.26	.06		.01	.16	.09	.05	.40
[d] Internal State Awareness	Correl.	.02	-.11		.22	-.11	.31*	.15	.16
	Sig.	.88	.48		14	.48	.04	.39	.27

[a] *Correlations, with levels of significance, reported for women, n = 353 (Miller et al., 1981)*

[b] *Correlations, with levels of significance, reported for combined genders, n = 452 (Fenigstein et al., 1975)*

[c] *Correlations, with no p values given, reported for combined genders, n = 628 (Miller et al., 1981)*

[d] *Sub-division of Private Self-consciousness (Anderson et al., 1996)*

**significant at the 5% level* ***significant at the 1% level*

Table 3.3 Multiple Regression (entry method) with Self-objectification as the Dependent Variable

Predictor	Adjusted R^2	ΔR^2	β
Step 1			
Interoceptive Accuracy			-.31
(Sig.)			(.03*)
	.08		
	(.03*)		
Step 2			
Interoceptive Accuracy			-.28
(Sig.)			(.03*)
Public Body Consciousness			.45
(Sig.)			(.00**)
	.27	.19	
	(.00**)		
Step 3			
Interoceptive Accuracy			-.28
(Sig.)			(.03*)
Public Body Consciousness			.47
(Sig.)			(.00**)
Private Body Consciousness			-.23
(Sig.)			(.07)
	.31	.04	
	(.00**)		

**significant at the 5% level*

***significant at the 1% level*

Participants' average heart rates were recorded over the three heartbeat perception trials, as a proxy for physical arousal. Average heart rate was significantly correlated with Social Anxiety, $r = .34$, $p = .02$, and also with Body Competence, $r = -.36$, $p = .02$. However, there were no significant correlations between heart rate and the variables in the multiple regression (Self-objectification, $r = .12$, $p = .43$; interoceptive accuracy, $r = -.16$, $p = .28$; Public Body Consciousness, $r = -.05$, $p = .73$; and Private Body Consciousness, $r = .14$, $p = .35$), indicating that participants' physical arousal is unlikely to have influenced the findings.

Average heart rate and the interaction of heart rate with interoceptive accuracy were added to the multiple regression as potential confounding variables but were nonsignificant and added nothing to the explanatory power of the model.

3.2.4 Discussion

In their theory of self-objectification, Fredrickson and Roberts made the previously untested claim that gender differences in interoceptive accuracy are the direct result of women's tendency to self-objectify (Fredrickson & Roberts, 1997). This is the first study to investigate that prediction using a heartbeat perception method. Interoceptive accuracy in women students was compared with scores on the Self-objectification Questionnaire (Fredrickson et al., 1998), the Self-consciousness Scale (Fenigstein et al., 1975) and the Body Consciousness Scale (Miller et al., 1981). Interoceptive accuracy was significantly negatively correlated with Self-objectification scores, as expected. Self-objectification in women was significantly predicted by a combination of interoceptive accuracy, Public Body Consciousness and Private Body Consciousness, which together explained 31% of the variance in the Self-objectification scores. It is not clear from this experiment why some women are more liable to self-objectify than others. However, the results indicate that low interoceptive accuracy is a predisposing factor, rather than an outcome, of high self-objectification, as hypothesised in this experiment but contrary to Fredrickson and Roberts' original suggestion. In confirming this prediction, Experiment 3 adds to the research linking interoceptive and exteroceptive representations of the body.

The results support an interpretation of interoceptive accuracy in terms of the capacity for attending to internal bodily signals. Potentially, women for whom interoceptive stimuli are experienced as less salient have a greater tendency to direct their attention to their bodies from an exteroceptive, third-person perspective and are therefore vulnerable to self-objectification. Fredrickson and Roberts' explanation of the link they expected would exist between self-objectification and interoceptive accuracy was that women who self-objectify are using up limited attentional resources on their bodies as perceived from a third-person perspective and so have less attention available for interoceptive signals (Fredrickson & Roberts, 1997). Pennebaker, in his 'competition of cues' hypothesis, similarly argued that when both internal and external sources of information are available, attention paid to one reduces attention paid to the other (Pennebaker, 1982). He made the crucial point that individuals direct their attention in accordance with their judgment of the salience and importance of internal or external stimuli (Pennebaker

& Lightner, 1980). The implication is that women who self-objectify judge external aspects of the self (e.g. the body as perceived by a real or imagined audience) as more salient than their interoceptive cues. This can be explained within a theory that the self is the product of the optimal integration of all self-relevant cues - interoceptive, exteroceptive and narrative (Apps & Tsakiris, 2013). If people with low interoceptive accuracy are characterised as having less reliable and salient interoceptive cues, it follows that they will accord more weight to exteroceptive cues. Cultural attitudes to women’s bodies may then render such women particularly vulnerable to self-objectification and body shame.

The observed relation between low interoceptive accuracy and high Self-objectification has potential significance for emotional experience and resonates with reports of low interoceptive accuracy in disorders involving negative affect. High Self-objectification is linked to negative affect (Miner-Rubino et al., 2002) and to depressive symptoms (Peat & Muehlenkamp, 2011; Szymanski & Henning, 2006; Tiggemann & Kuring, 2004). Similarly, low interoceptive accuracy is associated with moderate depression (Dunn et al., 2007) and has been reported in a number of clinical conditions, such as anorexia (Pollatos et al., 2008), alexithymia (Herbert et al., 2011) and depersonalisation disorder (Sedeño et al., 2014). There is a wealth of evidence to suggest that individuals with high interoceptive accuracy experience more emotional arousal, for the same objective bodily arousal, than people with low interoceptive accuracy (Barrett & Bar, 2009; Herbert, Pollatos, et al., 2007; Wiens, 2005). The results of Experiment 3 imply that women who self-objectify are those who are relatively unaware of the interoceptive cues which are related to their emotions and who may also therefore experience emotion less intensely (Myers & Crowther, 2008). Such women may be vulnerable to clinical conditions associated with poor interoceptive accuracy, such as anorexia, alexithymia and somatoform disorders. For example, poor emotional awareness, as measured by the Toronto Alexithymia Scale (Bagby, Parker, & Taylor, 1994), mediates between Self-objectification and eating disorders, (Muehlenkamp & Saris-Baglama, 2002).

Interoceptive accuracy cannot capture potentially important aspects of body awareness that are measured by self-report instruments, such as the individual’s feelings about bodily signals or her tendency to ruminate on such sensations. However, the use of a heartbeat perception measure of body awareness could potentially be successful within objectification research, in view of the measure's applicability and validity in a wide range of research into interoception, emotional experience and disordered experience of the self.

Public Body Consciousness, which was the second predictor of Self-objectification in Experiment 3, may also be a factor in the link between Self-objectification and negative affect. In women, Public Body Consciousness correlates with negative emotionality (Miller et al., 1981) which is the tendency to get angry, upset or frightened, as measured by the emotionality subscale of the Emotionality, Activity, Sociability, Impulsivity, Temperament Scale (Buss & Plomin, 1975). As a predictor of Self-objectification, Public Body Consciousness may represent a measure of the tendency to experience negative affect.

Somewhat surprisingly, the third significant predictor of Self-objectification in the regression equation was Private Body Consciousness. Private Body Consciousness predicted Self-objectification independently of interoceptive accuracy and the two measures did not correlate. This suggests that while Private Body Consciousness is significantly correlated with Self-objectification, it is measuring something other than awareness of the inner body. Support for this idea is provided by the many studies that have attempted to use Private Body Consciousness as a measure of internal body awareness in mediating between Self-objectification and negative affect or eating disorders (Myers & Crowther, 2008). Success depends on the choice of instrument with which body awareness is measured. Studies using Private Body Consciousness generally report no effect (Muehlenkamp & Saris-Baglama, 2002; Szymanski & Henning, 2006; Tiggemann & Slater, 2001). One successful study (Myers & Crowther, 2008) used the Interoceptive Awareness scale of the Eating Disorders Inventory (Garner, Olmstead, & Polivy, 1983). This scale is made up of items that assess awareness of emotions e.g. 'When I am upset, I don't know if I am sad, frightened, or angry' and others that assess feelings of hunger and satiety e.g. 'I get confused as to whether or not I'm hungry'. It was reported that the questions specific to hunger accounted for this instrument's success as a mediating variable (Myers & Crowther, 2008). In the light of the many nonsignificant results obtained with most questionnaire measures of internal body awareness, it is surprising that physiological measures of internal body awareness have so rarely been used in objectification research.

Experiment 3 also explicitly tested the assumption, frequently made in the self-objectification literature, that Self-objectification is related to Public Self-consciousness and Public Body Consciousness. These two scales are designed to measure the individual’s awareness of herself as perceived from a third-person perspective (Miner-Rubino et al., 2002). Public Self-consciousness is a measure of an individual’s thoughts and feelings about how other people perceive her (e.g. ‘I am concerned about what other people think of me’), whereas public body consciousness is specifically related to body awareness (e.g. ‘I’m concerned about my posture’). It therefore seemed probable that the Public Self-consciousness would be linked to Self-objectification, which is defined as the tendency to perceive and judge one’s body from a third-person perspective. As expected, the results show that 27% of the variance in Self-objectification scores was predicted by interoceptive accuracy and Public Body Consciousness taken together but that Public Self-consciousness was not significantly correlated with either interoceptive accuracy or Self-objectification in this study and did not contribute to the regression model.

Private Body Consciousness has frequently been used in self-objectification research as a proxy for body awareness but in this experiment it was not significantly correlated with interoceptive accuracy. Not only were interoceptive accuracy and Private Body Consciousness uncorrelated here but they were also independent predictors of Self-objectification (with low Private Body Consciousness scores and low interoceptive accuracy both predicting high Self-objectification). This implies that the two measures tap into different, but perhaps complementary, aspects of internal body awareness. It may explain why many studies in the self-focus literature that have attempted to find paths from Self-objectification to eating disorders and other negative outcomes, through the mediating effect of Private Body Consciousness (as a measure of body awareness), have reported nonsignificant results (Myers & Crowther, 2008).

Experiment 3 had several limitations. Participants were well-educated young women, whose habitual tendencies to self-focus may not be typical of a broader population. However, the various self-report measures (and their inter-correlations) fell within the range of values previously published for these instruments and therefore appear representative. The primary purpose of the study was to investigate interactions between interoceptive and exteroceptive representations of the body, by testing Fredrickson and Robert's claim that self-objectification is linked to heartbeat perception in women (Fredrickson & Roberts, 1997). The experiment therefore used only the Self-objectification Questionnaire (Fredrickson et al., 1998), Self-consciousness Scales (Fenigstein et al., 1975) and Body Consciousness Questionnaire (Miller et al., 1981), which have all been widely used to study self-focus. To establish the potential value of using heartbeat perception as a mediating variable between Self-objectification and disordered eating it would necessitate the use of measures such as Body Shame, and Body Surveillance (McKinley & Hyde, 1996) and the Eating Disorders Inventory (Garner et al., 1983) which were not included in this experiment. Future research is required to address two further limitations of this study. Firstly, male participants were not tested, who may present a different pattern of relationships. Secondly, participants were not screened for the possible presence of eating disorders, which are prevalent in young women (Peat & Muehlenkamp, 2011). These would have had a mediating effect (Baron & Kenny, 1986) on the relationship found here between self-objectification and interoceptive accuracy because people with eating disorders tend to have relatively low heartbeat perception (Pollatos et al., 2008) but are also more prone to self-objectify (Calogero, Davis, & Thompson, 2005).

3.2.5 Conclusion

This study is the first to test Fredrickson and Robert's claim that interoceptive accuracy in women, as measured by heartbeat perception, is negatively correlated with self-objectification. Interoceptive accuracy, together with Public Body Consciousness and Private Body Consciousness, accounted for 31% of the variance in scores on the Self-objectification Questionnaire. The experiment extends the growing literature on interaction between interoceptive and exteroceptive representation of the self and supports the proposal that interoceptive accuracy measures attention to interoceptive representations of the body. The strength and salience of these, in women with high interoceptive accuracy, potentially serve to protect the individual against a tendency to self-objectify.

Chapter 4. Interoceptive Accuracy and Self/Other Distinction in Action

4.1 General Introduction

Despite recent investigation of the effect of interoceptive accuracy in multisensory contexts and self-processing (Aspell et al., 2013; Suzuki et al., 2013), little is known about the potential role of interoception in the action system. This lack of empirical research is striking, given that human actions are thought to be driven by the goal of homeostatic control, which is signalled interoceptively (Craig, 2010; Damasio, 2010; Seth, 2013). Theoretical accounts of the neural basis of perception and action stress their inter-connectedness, proposing that action is coded in terms of its sensory consequences (Catmur, Walsh, & Heyes, 2009; Karl Friston, 2009; Hommel, 2009; Schütz-Bosbach & Prinz, 2007). It has previously been assumed that the sensory consequences of an action are primarily exteroceptive. However, empathy for pain (Avenanti et al., 2005; Singer et al., 2004) and overlapping cortical activation during the experience, observation or imagination of disgust (Wicker et al., 2003) can only be explained if actions also involve a representation of their interoceptive sensory consequences (Heyes & Bird, 2007).

The evidence suggests that people with low interoceptive accuracy experience greater ‘self/other overlap’ in multisensory contexts, for example in identifying their own hand during the rubber hand illusion (Tajadura-Jiménez & Tsakiris, 2013; Tsakiris et al., 2011). Self/other overlap has been defined as ‘any phenomenon whereby an observer engages a state similar to that of the target, via activation of the observer’s personal representations for experiencing the observed state, whether through direct perception or simulation’ (Preston & Hofelich, 2012). Experiments 4 and 5 were therefore concerned with the potential effect of interoceptive accuracy in two experimental paradigms that are assumed to engage shared representations in the motor domain.

Experiment 4 employed ‘the social Simon task’ (Sebanz, Knoblich, & Prinz, 2003), hypothesising that people with low interoceptive accuracy, who potentially experience more self/other overlap in multisensory contexts, would have a greater tendency to represent the actions of a coactor, as indexed by the social Simon effect.

Experiment 5 examined whether interoceptive accuracy is related to ‘automatic imitation’ (Heyes, 2011), which depends on an observer’s tendency to imitate an observed, task-irrelevant action. Automatic imitation is similarly assumed to involve self/other overlap and, intriguingly, the tendency to imitate is reduced when self-focus is enhanced using either a mirror or self-relevant narrative information (Spengler, Brass, Kühn, & Schütz-Bosbach, 2010), It was hypothesised that people with low interoceptive accuracy would have greater difficulty resisting automatic imitation.

4.2 Experiment 4. Interoceptive Accuracy and the ‘Social Simon Effect’: Representing the Actions of Other People.

4.2.1 Introduction

Theories about the origins of the self have tended to ignore the role of social interaction in human evolution. However, early hominids may have gained a sense of ‘self in action’ by engaging in joint action and imitation with their fellows (Sebanz, 2007). An important aspect of any joint action is that individuals must be able to represent their own precepts and actions, as well as simulating those of the other people involved, in order to coordinate their different movements. This is essential if they are to arrive at an outcome that is more than the sum of its parts, for example, during a cooperative hunt (Sebanz, 2007). According to embodied simulation accounts, we understand the actions and emotions of other people by activating our own cortical representations for the same behaviour or affect, using our bodies by way of analogy (Gallese & Sinigaglia, 2011). These shared representations result in self/other overlap, which is assumed to account for ‘the social Simon effect’.

In a classic Simon task (Simon & Rudell, 1967) participants are required to respond to a nonspatial physical feature (such as a colour or a shape) by, for example, pressing a left or right key while ignoring the location (left or right) in which the stimulus is presented. ‘The Simon effect’ refers to the robust finding that responses are faster when the stimulus location and the required response occur in the same location (are congruent) than when they are incongruent. This difference in mean reaction times is known as the ‘congruency effect’ (Hommel, 2011).

Sebanz, Knoblich and Prinz (2003), developed a ‘social’ variant of the Simon task to demonstrate the effects of joint action with a partner. They used a go-nogo task that required the participant to make a left or right button press in response to a go stimulus (the red or green colour of a finger ring), while simultaneously inhibiting responses to a neutral cue (the nogo stimulus), which was the direction in which the finger was pointing. The task was performed in three conditions. In the ‘two-choice condition’ participants were told to respond to both colours (e.g. to press the left button when the finger ring was green and the right button when it was red). In the ‘individual condition’ the participants were required to respond only to one colour cue (e.g. to press the left button when the ring was green but not to respond to red cues). In the ‘social condition’ they sat alongside a coactor (the experimenter) and once more responded to only one colour cue, while the experimenter responded to the other (Sebanz, Knoblich, & Prinz, 2003).

People generally show a reliable spatial compatibility (Simon) effect in the two-choice condition, i.e. they respond faster in the ‘congruent condition’, when the finger points towards the button they are required to press and they have slower RTs when the trial is ‘incongruent’. However, in the individual condition, when people respond to one colour only, the effect of congruency disappears. The crucial finding in Sebanz et al.’s (2003) original experiment was that the congruency effect reappeared in the social condition. They attributed this to the participant mentally representing the coactor’s task, which then conflicts with their own task. The congruency effect in the social Simon condition has consequently been taken as an index of the degree to which people co-represent the actions of a coactor (Hommel, 2009; Sebanz et al., 2003). If this explanation is correct and participants represent the actions of the coactor, they must then separate their representation of their own action from their representation of the other person’s action. Assuming that interoceptive accuracy affects the ability to make self/other distinctions in the sensory domain, potentially it is similarly linked to the ability to separate self and other in the motor domain.

However, the social Simon effect is modulated by top-down social influences that might act as confounds, by influencing the desire to cooperate with the coactor (and thus to represent their actions). The effect can disappear completely if the coactor is intimidating or competitive (Hommel, Colzato, & Wildenberg, 2009). Conversely, it may be enhanced by priming participants with pronouns that produce a sense of self-other integration (Colzato, van den Wildenberg, & Hommel, 2013). Similarly, priming with instances of an interdependent versus independent self-construal increases the social Simon effect (Colzato, de Bruijn, & Hommel, 2012). As checks on two of the most obvious of these potential top-down effects, the Revised Self-monitoring Scale (Lennox & Wolfe, 1984) and the Interpersonal Orientation Scale (Swap & Rubin, 1983) were administered to all participants. Individuals who are high in self-monitoring (Lennox & Wolfe, 1984) find social aspects of the environment particularly salient. It is therefore possible that such people would have a greater tendency to represent the actions of a coactor in the social Simon task. Similarly, people with high interpersonal orientation are more likely to attend preferentially to the actions of a partner and thus to mentally represent their actions (Swap & Rubin, 1983).

In Experiment 4, two sets of visual stimuli were employed for the Simon task (Figure 4.1), which were tested for all participants in all three conditions (two-choice, individual and social). The pictures of pointing hands were kindly provided by Professor. Natalie Sebanz, (Sebanz, Rebbechi, Knoblich, Prinz, & Frith, 2007; Sebanz et al., 2003). The Simon effect is typically investigated using coloured geometric shapes that appear either on the left or the right of the screen (Hommel et al., 2009). The ‘social Simon effect’, by contrast, was first demonstrated with the pointing hand stimuli shown in Figure 4.1 (Sebanz et al., 2003). These differ from the more typical geometric stimuli in (i) appearing centrally and therefore relying on pointing, rather than screen position, to give directional cues; and (ii) having a social connotation. Given that the social Simon effect is assumed to involve mentally representing the actions of the experimental partner, pointing hand stimuli potentially introduce the hand actions of yet a third actor. For comparison, therefore, in Experiment 4 participants were also tested using directional arrows, which have no social/human connotation.

Congruency effects were calculated as the difference between mean reaction times on congruent and incongruent cues. These were compared with interoceptive accuracy, assessed using the Mental Tracking Method. Gender, body mass index

(BMI), and resting heart rate were recorded, as possible confounds of the heartbeat perception task (Cameron, 2002). All participants completed the Revised Self-monitoring Scale (Lennox & Wolfe, 1984) and the Interpersonal Orientation Scale (Swap & Rubin, 1983). A criticism of the Mental Tracking Method is that participants may estimate the elapsed time interval to guess the correct number of heartbeats. Therefore individuals were also asked to estimate the length of three, randomly presented, intervals (Dunn et al., 2010).

The principal hypothesis of Experiment 4 was that people with low interoceptive accuracy would demonstrate a larger congruency effect in the social Simon condition, compared with good heartbeat perceivers. It was reasoned that all participants would, to some extent, form a motor representation of the coactor's action. However, if poor heartbeat perceivers are less good at making self/other distinctions, then these representations would be more likely to interfere with their performance of their own task, resulting in a larger social Simon effect.

A second hypothesis proposed that individuals high in self-monitoring and in interpersonal orientation would exhibit greater congruency effects in the social Simon condition but not on the two-choice or individual conditions. Good heartbeat perceivers are better able to down-regulate affect (Füstös et al., 2012), which might imply that they would score higher on self-monitoring scales. Moreover, high interoceptive accuracy has been linked to empathy (Ernst, Northoff, et al., 2013; Fukushima et al., 2011), which is potentially associated with interpersonal orientation. A third hypothesis therefore anticipated that scores on these two scales might mediate the link that the experiment anticipated would be found between interoceptive accuracy and the social Simon effect.

4.2.2 Method

4.2.2.1 Participants

49 students at Royal Holloway participated for course credit. One was excluded for failing to comply with the instructions and two for making more than 15% errors in the two-choice condition. Of the remaining 46 participants (10 male), the mean age was 21.0yrs, (SD = 3.1). All declared themselves right-handed. The experiment

received approval from the Ethics Committee of the Psychology Department, Royal Holloway University of London.

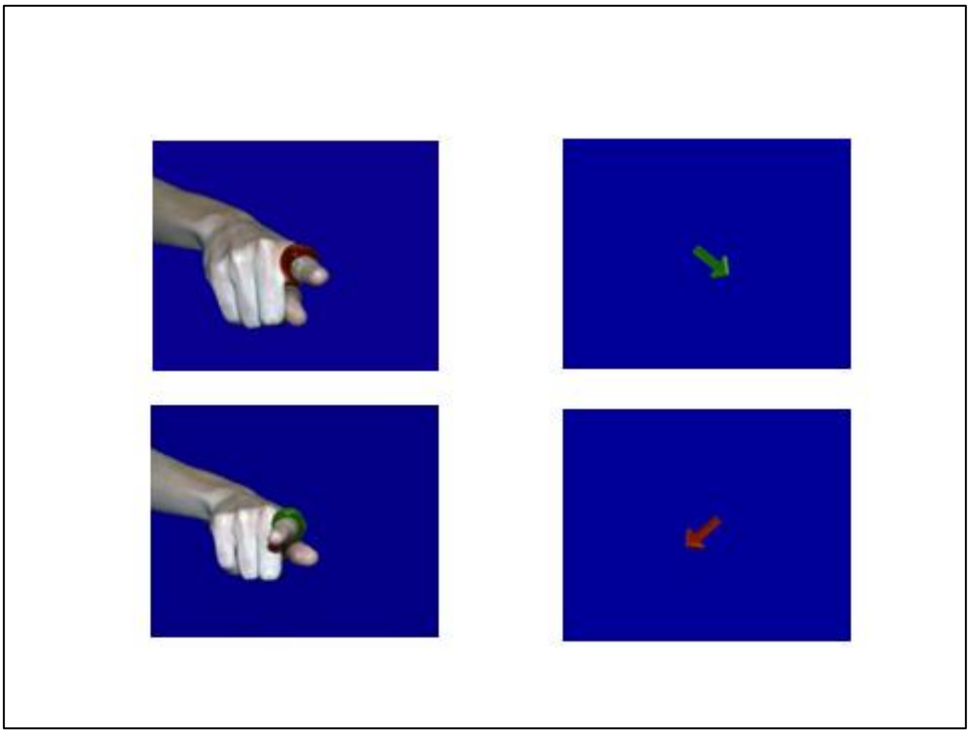
4.2.2.2 Procedure

Participants were asked to report their age, gender, weight and height. Body mass index (BMI) was calculated in the usual way. Participants first completed the Mental Tracking task. They then performed the Simon task (section 4.2.2.6) in all three blocked conditions, the order of which was randomised. Finally they completed the two questionnaires.

4.2.2.3 Interoceptive Accuracy and the 'Time Modulus' Measure

Interoceptive accuracy (IA) was measured using the Mental Tracking Method (Schandry, 1981), as described in Experiment 2 (sections 2.2.2.3 and 2.2.2.4). Participants were also asked to estimate the length of three randomly presented intervals (19s, 37s and 49s). A measure of accuracy in estimating elapsed time (the 'time modulus') was calculated from these three estimates, using the formula $\{1/3\ \Sigma\ [1 - (|\text{true length of interval} - \text{reported length of interval}|\ /\text{true length of interval})]\}$ (Dunn et al., 2010). This variable was for use as an extra regressor in any regression analyses involving interoceptive accuracy.

Figure 4.1 Examples of the Stimuli



4.2.2.4 Stimuli

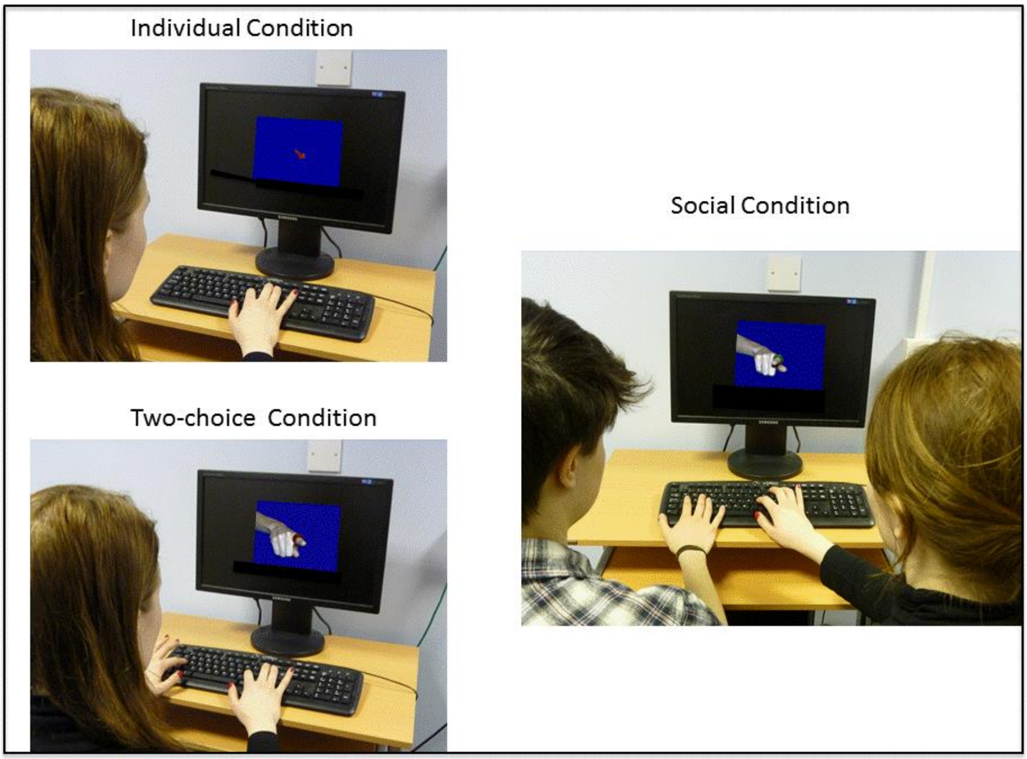
Participants were required to respond to two sets of cues (Figure 4.1). The ‘arrow’ stimuli were a red or green arrow pointing either to the left or the right (at an angle of 45% to the horizontal). The ‘hand’ stimuli were pictures of a right hand, wearing either a red or a green coloured ring on the index finger, which was pointing either to the left or the right (similarly at an angle of about 45%). The length of the arrow was matched to the length of the finger (3cm). The stimuli appeared on a blue background (14cm x 17 cm), which was presented in the centre of a black screen.

4.2.2.5 The Simon Task

All stimuli were presented on a standard PC. In the individual and two-choice conditions of the Simon task the participant sat centrally at the computer, approximately 60cm from the screen, while the experimenter sat on the participant’s left, at a distance of about 1.5m. In the social condition the participant sat right of centre, about 60cm from the coactor/experimenter, who sat on their left (Figure 4.2) The experimenter was present in the lab during all three of the conditions, sitting 2m behind and to the left of the participant, except in the joint condition which was shared with the participant. All instructions were delivered, and behavioural responses recorded, using Presentation software (Neurobehavioral Systems, Albany, CA) on a standard desktop PC.

All participants completed all three blocked conditions, which were presented in random order. In the individual and social conditions the participants responded with their right hand only, by pressing the ‘L’ key on the computer keyboard. Even-numbered participants were required to respond to green cues (with the right hand) and odd-numbered participants to red cues.

Figure 4.2 Examples of the three Experimental Conditions



Each trial lasted 1.7s, consisting of a blank screen for 200ms, stimulus presentation for 500ms, followed by a blank screen for 1000ms. After eight practice trials, each of the eight stimuli (arrow/hand, green/red, pointing to left/right) was presented 32 times, in fully randomised order. In the two-choice condition, the participants responded to all 256 trials by pressing the ‘L’ key on the computer keyboard with the right hand and the ‘A’ key with the left hand. In the social and individual conditions, they responded with their right hand only using the ‘L’ key, to half the presented stimuli (i.e. to one colour only, on 128 trials). Participants were told that the task was a test of speed and accuracy and were instructed to work as fast as possible without making mistakes.

4.2.2.6 Questionnaires

The Revised Self-monitoring Scale

The Revised Self-monitoring Scale (Lennox & Wolfe, 1984) is made up of 13 items and is divided into two subscales: (a) The Ability to Modulate Self-presentation, for example, ‘Once I know what the situation calls for, it's easy for me to regulate my actions accordingly'; and (b) Sensitivity to the Expressive Behaviour of Others, for example, 'In conversations, I am sensitive to even the slightest change in the facial expression of the person I'm conversing with'.

The Interpersonal Orientation Scale

The Interpersonal Orientation Scale (Swap & Rubin, 1983) consists of 29 questions, for example, 'I am interested in knowing what makes people tick' and 'When someone does me a favour I don't usually feel compelled to return it'. Question 29 ('I find myself wondering what telephone operators are really like') was omitted as outdated.

On both questionnaires, participants were asked to rate how true (how descriptive) each statement was for them. Responses were recorded on a 5-point Likert scale, with 1 being 'not at all true' and 5 'completely true'.

4.2.3 Results

4.2.3.1 Interoceptive Accuracy and Confounds

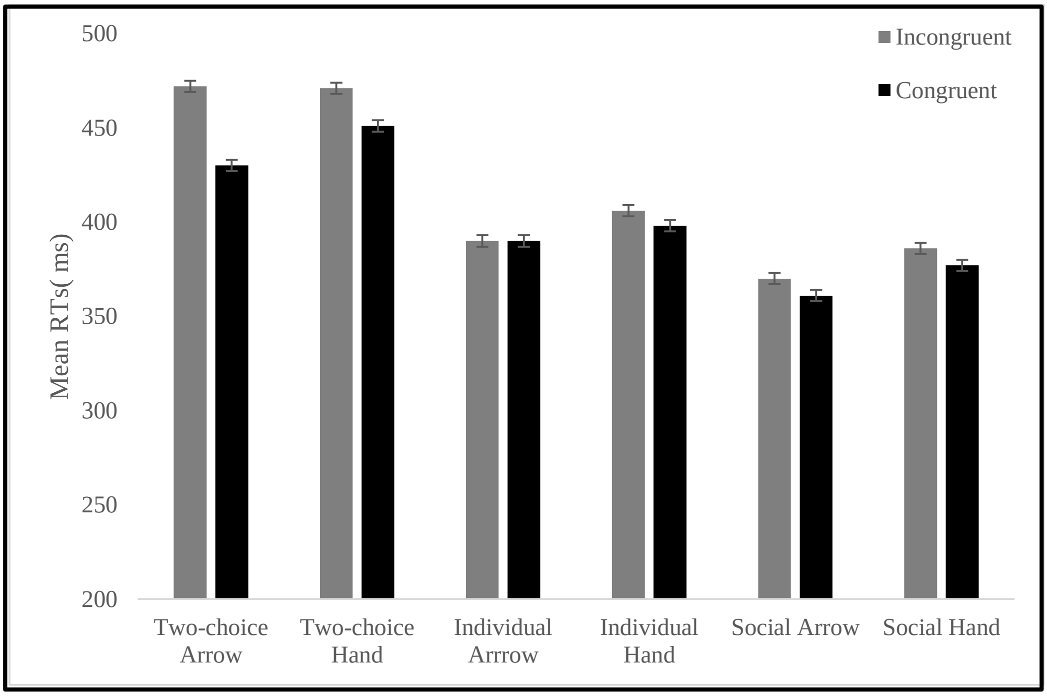
The 'time modulus' measure (of participants' ability to estimate the length of an elapsed interval) was correlated with interoceptive accuracy, $r = .30$, $p = .05$. Major critics of the Mental Tracking Method have reported that the participants can perform well on the task if they are good at estimating elapsed time and are not reporting counted heartbeats but simply counting seconds (Ring & Brener, 1996). The positive correlation between the time modulus measure and interoceptive accuracy was therefore noted as a potential confound of any significant findings in this experiment.

As reported elsewhere (Cameron, 2001; Fairclough & Goodwin, 2007; Knapp-Kline & Kline, 2005; Stevens et al., 2011), people with high interoceptive accuracy tend to have slower heart rates but in this experiment this did not reach significance, $r = .27$, $p = .07$. Body mass index (BMI) has been shown to influence heartbeat perception (Cameron, 2001) but all participants had BMI within the normal range and BMI was not correlated with interoceptive accuracy, $r = .15$, $p = .32$.

4.2.3.2 Reaction Time Analysis of the Simon Task

In every condition, errors were omitted from the analysis. There were two sources of errors. Firstly, any trial was removed where the participant pressed the incorrect button. Secondly, reaction time (RT) outliers of less than 200ms or more than 900ms were also omitted (Sebanz, Knoblich, Stumpf, & Prinz, 2005). The data for two participants was excluded from the analysis because they made excessive numbers of errors (more than 15% in the two-choice condition). The average rate of errors for the remaining participants was 2.8% in the two-choice condition and 1.2% in the individual condition. These error rates as well as mean RTs (Figure 4.2) are close to the values reported by Sebanz et al. (2003).

Figure 4.3 Mean Reaction Times by Stimulus and Condition (error bars represent SEM



Participants were divided into a high IA group (above median) and a low IA group (below median), using a median split (median IA = .6). Repeated measures ANOVA was performed with the three conditions (two-choice, individual or social), congruence (congruent vs. incongruent trials) and the nature of the stimulus (arrows vs. hands) as within-subjects variables. Interoceptive accuracy group (high vs. low), gender and the colour to which the participant responded (with their right hand) were between-subjects variables. Mauchley’s test of Sphericity was nonsignificant. There were the anticipated main effects of condition, *F*(2, 88) = 87.0, *p* < .001, and of whether trials were congruent or incongruent, *F*(1, 44) = 68.4, *p* < .001, confirming the existence of Simon effects. There was also a main effect of stimulus type *F*(1, 44) = 45.8, *p* < .001, indicating that the arrow and hand stimuli elicited different reaction times. There was no interaction of IA group with condition, *F*(2, 88) = 1.92 *p* = .16; or with congruency *F*(1, 44) = 0.23, p = .88; or with stimulus type *F*(1, 44) = 0.10, *p* = .75, implying that IA group had no effect within the analysis. There was the expected interaction of condition and congruency (whether the trials were congruent or incongruent), *F*(2, 88) = 17.0, *p* < .001. There was also an interaction of condition and stimulus type, *F*(2, 88) = 4.12, *p* = .01, indicating that the arrow and hand stimuli had different effects depending on the condition. No other interactions were significant. There was no main effect of IA group, *F*(1, 38) = 0.10, *p* = 75; gender, *F*(1, 38) = 0.8, p = .37; or the colour to which the participant responded, *F*(1, 38) = 1.2, *p* = .28.

To explore this further, repeated measures ANOVA was performed in each condition separately, for the stimulus type (arrow vs. hand) separately, with mean RTs (congruent vs. incongruent trials) as within-subjects variable. Between-subjects variables were: gender; interoceptive accuracy group (high vs. low); the colour to which the subject responded with their right hand (red vs. green); and the order in which the particular condition was presented (first, second or third).

Two-choice Condition

Mauchley's test of Sphericity was nonsignificant. For both the arrow and hand stimuli, there were the expected congruency effects, i.e. longer RTs for incongruent than congruent stimuli (Table 4.1). There were no interactions of congruency effect with IA group. There was likewise no effect of the order (first, second or third) in which the two-choice condition was presented. There was no correlation between interoceptive accuracy and the congruency effect, for either the hand stimuli, *r* = .07, *p* = .64, or the arrow stimuli, *r* = -.12, *p* = .45, nor was there a correlation between interoceptive accuracy and any mean RT, *p* > .48.

Paired samples *t* tests showed that participants responded significantly faster to the arrow than to the hand stimuli, when these were congruent, $t(45) = 8.14$, $p < .001$, but not when they were the incongruent $t(45) = .31$, $p = .76$.

Table 4.1. Two-choice condition. Results of ANOVA

Two-choice condition	**Arrow**	**Hand**
Congruency effect	$F(1, 29) = 106.54$ $p < .001$**	$F(1, 29) = 8.4$ $p = .01$*
Interaction of the congruency effect with IA group	$F(1, 29) = 0.48$ $p = .50$	$F(1, 29) < .001$ $p = .98$
Interaction of the congruency effect and gender	$F(1, 29) = 2.93$ $p = .10$	$F(1, 29) = 2.38$ $p = .14$
Interaction of the congruency effect with the colour responded to with the right hand	$F(1, 29) = 0.39$ $p = .54$	$F(1, 29) = 0.58$ $p = .46$
Interaction of the congruency effect with the order of presentation of the two-choice condition	$F(2, 29) = 2.36$ $p = .12$	$F(2, 29) = 0.21$ $p = .82$

**significant at the 5% level*

***significant at the 1% level*

Individual Condition

For the arrow stimuli, as expected, there was no congruency effect. However, unexpectedly, for the hand stimuli there was a significant congruency effect (Table 4.2). There were no interactions with interoceptive accuracy group for either the arrow or hand stimuli.). The ten men had significantly shorter RTs than the women to the arrow but not to the hand stimuli. The colour to which the participant responded with the right hand had no effect. There was also no effect of the order in which the individual condition was presented (Table 4.2). Interoceptive accuracy was not correlated with either of the congruency effects, nor with any of the mean RTs in the individual condition, $p > .19$. Paired samples *t* tests show that participants were significantly faster when responding to the arrow compared to the hand stimuli, in both incongruent trials, *t*(45) = 5.35, *p* < .001, and congruent trials, *t*(45) = 2.52, *p* = .02.

Table 4.2 Individual condition. Results of ANOVA

Individual Condition	**Arrow**	**Hand**
Congruency effect	*F*(1, 29) = 2.63 *p* = .12	*F*(1, 29) = 6.16 *p* = .02*
Interaction of the congruency effect with IA group	*F*(1, 29) = 2.79 *p* = .11	*F*(1, 29) = 1.56 p = .23
Interaction of the congruency effect with gender	F(1, 29) = 5.60 *p* = .03*	*F*(1, 29) < 0.001 *p* = .96
Interaction of the congruency effect with colour responded to with the right hand	*F*(1, 29) = 0.79 *p* = .39	*F*(1, 29) < 0.001 *p* = .96
Interaction of the congruency effect with the order of presentation of the individual condition	*F*(2, 29) = 0.04 *p* = .96	*F*(2, 29) = 0.23 *p* = .80

**significant at the 5% level*

Social Condition

For both the arrow and the hand stimuli, as expected, there were significant congruency effects (Table 4.3). However, there were no interactions with interoceptive accuracy group). The main hypothesis of Experiment 4 was thus not confirmed. People with low interoceptive accuracy did not exhibit larger congruency effects (social Simon effects). Gender, the colour to which the participant responded with their right hand and the order in which the social condition was presented all had no significant effect.

Table 4.3 Social Condition. Results of ANOVA

Social Condition	***Arrow***	***Hand***
Congruency effect	*F*(1, 29) = 16.32 *p* = .001**	*F*(1, 29) = 16.40 *p* = .001**
Interaction of the congruency effect with IA group	*F*(1, 29) = 0.11 *p* = .74	*F*(1, 29) = 1.84 *p* = .19
Interaction of the congruency effect with gender	*F*(1, 29) = 1.79 *p* = .20	*F*(1, 29) < 0.001 *p* = .95
Interaction of the congruency effect with colour responded to with Right hand	*F*(1, 29) = 0.03 *p* = .88	*F*(1, 29) = 2.16 *p* = .16
Interaction of the congruency effect with the order of presentation of the social condition	*F*(2, 29) = 2.04 *p* = .16	*F*(2, 29) = 1.34 *p* = .28

**significant at the 5% level*

***significant at the 1% level*

Paired samples *t* tests showed that participants were again significantly faster in their response to the arrow stimuli than to the hands, on both the incongruent, *t*(45) = 7.03, *p* < .001, and congruent trials, *t*(45) = 8.00, *p* < .001. Interoceptive accuracy was not correlated with the congruency effects, nor with any of the mean RTs in the social condition, *p* > .53.

Table 4.4 Social Condition. Correlations of the Questionnaire Measures with IA, Mean RTs and the Congruency Effects

	Revised Self-monitoring Scale	**(a) Ability to Modify Self-presentation**	**(b) Sensitivity to the Expressive Behaviour of Others**	**Interpersonal Orientation Scale**
Interoceptive Accuracy	*r* = -.17 *p* = .27	*r* = -.09 *p* = .57	*r* = -.16 *p* = .28	*r* = -.06 *p* = .68
Arrow stimuli Mean RT on incongruent trials	*r* = .33 *p* = .02*	*r* = .27 *p* = .07†	*r* = .21 *p* = .17	*r* = -.09 *p* = .55
Arrow stimuli Mean RT on congruent trials	*r* = .35 *p* = .02*	*r* = .36 *p* = .01*	*r* = .14 *p* = .37	*r* = -.08 *p* = .61
Arrow stimuli Congruency effect	*r* = -.07 *p* = .65	*r* = -.25 *p* = .05†	*r* = .18 *p* = .22	*r* = -.03 *p* = .81
Hand stimuli Mean RT on incongruent trials	*r* = .36 *p* = .02*	*r* = .33 *p* =.02*	*r* = .18 *p* =.24	*r* = -.14 *p* = .35
Hand stimuli Mean RT on congruent trials	*r* = .33 *p* = .03*	*r* = .29 *p* = .05†	*r* = .18 *p* = .22	*r* = -.22 *p* = .14
Hand stimuli Congruency effect	*r* = .13 *p* = .41	*r* = .17 *p* = .27	*r* = .01 *p* = .96	*r* = .22 *p* = .15

**significant at the 5% level* *†significant at the 10% level*

4.2.3.3 Questionnaire Measures

Scores on the Revised Self-monitoring Scale (Lennox & Wolfe, 1984) were correlated with mean RTs in the social condition, partly confirming the second hypothesis of this experiment (Table 4.4). This was largely accounted for by the Ability to Modify Self-presentation subscale, indicating that people who were inclined to modify their self-presentation had slower overall mean reaction times to all the stimuli. However, these correlation would not survive Bonferroni corrections for multiple comparison (with a significance level of .002). The congruency effect for the arrow stimuli (but not the hands) was close to being significantly correlated with this scale. As expected, this was seen only in the social condition. In the two-choice and individual conditions, Ability to Modify Self-presentation was not correlated with any mean reaction time measure. Scores on the Interpersonal Orientation Scale (Swap & Rubin, 1983) were not significantly correlated with any mean reaction time, or congruency measure, in any of the three conditions. Contrary to the third hypothesis, there were also no significant relationships between any of the questionnaire measures and interoceptive accuracy.

4.2.4 Discussion

Using a within-subjects design, interoceptive accuracy was compared with the congruency effect in the Simon task in each of three conditions, comprising two-choice, individual and social conditions (Sebanz et al., 2003). Stimuli in the Simon task were of two types, which were directional arrows and pictures of a pointing right hand. In each case, the participant's task was to respond to the colour (red or green) of the arrow, or of a ring on the index finger of the hand, while ignoring the irrelevant cue, which was the direction in which the stimulus was pointing. In the two-choice condition participants responded on all trials with a right button press for one colour and a left button press for the other colour. In the individual condition they responded with a right button press to only one colour, while ignoring the other. In the social condition they shared the task with a coactor (the experimenter) who responded to one colour while they responded to the other. It was hypothesised that people with high interoceptive accuracy would show a smaller congruency effect on the social Simon task because they are assumed to make better self/other distinctions. This was not supported by the data.

Results showed the expected congruency effect in the two-choice and the social conditions, for both hand and arrow stimuli. In the individual condition, where no congruency effects are predicted, there was an unexpected congruency effect for the hands, which might indicate that the effects were at least partly driven by some undetected spatial aspect of the experimental set up, to which the presence of the experimenter may have contributed, thereby confounding the experiment. The participants were divided by median split into a high interoceptive accuracy group and a low interoceptive accuracy group. There was no interaction of interoceptive accuracy group with any congruency effect in any condition, for either set of stimuli. There were no significant correlations between interoceptive accuracy and any of the congruency effects, nor mean reaction times in any condition. The order in which the three conditions were presented and the colour the participant responded to (with their right hand) had no significant effect. Men were faster in the individual condition (for arrows) but the small number of male participants makes gender effects unreliable. In all three conditions, participants were significantly faster in reacting to arrows than to hand stimuli. Potentially the arrows were more obviously directional and incorporated a greater area of colour, making them more salient.

The second hypothesis in this experiment was partly supported. There were significant correlations between scores on the Revised Self-monitoring Scale and reaction times in the social Simon condition. High self-monitors had slower reaction times, on both congruent and incongruent trials, when they performed the task with a coactor i.e. in the social condition (but not when they performed alone in the two-choice and individual conditions). Such individuals appeared to have a greater tendency to mentally represent the actions of the coactor, resulting in a larger congruency effect, for the arrow stimuli only, that nearly reached significance. However, these correlations do not survive Bonferroni correction and, contrary to the third hypothesis, self-monitoring was not related to interoceptive accuracy and could not account for the observed lack of association between interoceptive accuracy and the social Simon effect.

The congruency effect in the social Simon task has been taken as an index of the degree to which people co-represent the actions of a coactor (Hommel, 2009;

Sebanz et al., 2003). EEG, for example, reveals more response inhibition on incongruent trials of the social Simon condition than during the individual condition, manifesting as larger amplitude of the P300 component and a greater negative deflection of the lateralised readiness potential on incongruent trials (Sebanz, Bekkering, & Knoblich, 2006; Tsai, Kuo, Jing, Hung, & Tzeng, 2006). However, interpretation of the social Simon effect has been hotly debated. For example, whether it is the result of the 'mere presence' of another person (Sebanz et al., 2003; Tsai et al., 2006) or requires that the coactor is human and takes an active role (Tsai & Brass, 2007; Tsai, Kuo, Hung, & Tzeng, 2008; Vlainic, Liepelt, Colzato, Prinz, & Hommel, 2010); or only happens if the coactor is in the participant's peripersonal space (Guagnano, Rusconi, & Umiltà, 2010).

In a major critique of the social Simon effect, Dolk and colleagues (2011) conducted a series of experiment to show that a congruency effect can be produced in the individual condition of the Simon task by any salient (human or non-human) stimulus that provides a spatial reference frame which encourages the coding of the participant's actions as 'left' or 'right'. For example, a waving model cat, or even a silent metronome, is capable of producing a congruency effect, which cannot be attributable to a mental presentation of a coactor's actions because there is no coactor in the individual condition (Dolk, Hommel, Prinz, & Liepelt, 2013; Dolk et al., 2011). The unexpected congruency effect observed in Experiment 4 for the hand stimuli in the individual condition might be attributable to some similar spatial effect, such as the presence of the experimenter, which was a major design flaw and confound of the experiment.

None of these experiments conclusively resolves the question of whether, and to what extent, the social Simon effect involves the participant mentally representing the coactor's actions, but they imply that the causes of the social Simon effect are not as clear-cut as originally suggested (Dolk et al., 2011). If the effect relies on spatial attention then no interaction with interoceptive accuracy can be expected.

A final possibility is that, while the task does involve the participant forming a motor representation of the coactor's movement, individual differences in self/other distinction at the preconscious level of motor plans are outweighed by top-down contextual influences, such as how much the participant liked, or wished to cooperate with, the coactor (Hommel, 2011). The experiment was thus confounded by both spatial and social effects, which could not be controlled and are likely to have undermined the results.

4.2.5 Conclusion

The results of Experiment 4 indicate that interoceptive accuracy does not interact with the social Simon effect. There are a number of possible interpretations. The assumption that participants in the social Simon task mentally represent their coactor's task may be incorrect. There is much cogent criticism and empirical evidence to suggest that the task is flawed and that the effect can be accounted for by any salient stimulus (such as a coactor seated on their left) that biases the participants' attention, so that their own task becomes coded in spatial terms of left/right. Further research was warranted with another paradigm that is not confounded in this manner.

4.3 Experiment 5. Self/Other Distinction in Automatic Imitation[4]

4.3.1 Introduction

Experiment 4 assessed whether interoceptive accuracy modulates the extent to which people represent the actions of a confederate during joint action and found no link. However, the social Simon task is potentially confounded by the salience of the coactor, whose presence may cause the participants to code their actions spatially. A well-validated tool for measuring how effectively the self can be distinguished from other in the domain of action is provided by ‘automatic imitation’ (Spengler, von Cramon, & Brass, 2009). Experiment 5 therefore investigated whether the ability to inhibit imitation is modulated by interoceptive accuracy.

Automatic imitation refers to the human tendency to involuntarily imitate actions that we observe. Thus when an individual is required to perform a given action, observing another person perform an identical action typically facilitates performance, whereas observing a different action generally interferes with it, even when the observed action is entirely task-irrelevant (Heyes, 2011). Although the term ‘automatic imitation’ is commonly used, the phenomenon rarely involves true imitation, in that people seldom perform the wrong action. They must, however, resist a tendency to copy the action they observe. The ability to inhibit imitation is measured by the congruency effect, which is the difference between the slower mean reaction times (RTs) typically found when the required and observed actions are incongruent (i.e. different) and the faster mean RTs when the desired and observed actions are congruent, compared with the baseline condition of no observed action (Brass, Bekkering, & Prinz, 2001).

According to the Theory of Event Coding, automatic imitation occurs because actions are coded in terms of their goals and thus their sensory consequences. The distinction between perception and action is thus a false dichotomy (Hommel, Müsseler, Aschersleben, & Prinz, 2001). The Associative Sequence Learning (ASL) theory (Catmur et al., 2009) suggests that visual and motor components of

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actions are linked by long-term stimulus response (SR) bonds, such that the activation of a visual representation necessarily predicts a motor representation (Heyes, 2011). In support of this is has been shown that observing an action causes sub-threshold activation of an imitative response, which can be recorded in the peripheral motor system (Luciano Fadiga, Craighero, & Olivier, 2005). Automatic imitation is specific to the particular action and to the body part observed (Gillmeister, Catmur, Brass, & Heyes, 2008; Lamm, Batson, & Decety, 2007) and is enhanced when the observed action is seen from a first-person perspective. More recently, the theory of predictive coding links perception and action within a unified framework that may, in future, elucidate the neural mechanisms behind automatic imitation (Adams, Shipp, & Friston, 2012; K Friston, 2010).

Automatic imitation is therefore another example of a process that involves self/other overlap (Preston & Hofelich, 2012), whereby observers activate their own bodily representations of, for example, an action or an emotion, analogously to the state they observe in the other person (Gallese & Sinigaglia, 2011). These shared representations occur at a very early, preconscious processing stage. Thus, seeing hand movements increases cortico-spinal excitability and decreases the threshold at which transcranial magnetic stimulation (TMS) elicits motor evoked potentials (MEPs) from the specific muscles involved in that movement (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Moreover, priming participants with examples of interdependent self-construal increases the amplitude of MEPs elicited by TMS (Obhi, Hogeveen, & Pascual-Leone, 2011), indicating that these top-down influences act on cortical excitability in the motor areas that produce imitation. Furthermore, observing an action has the effect of increasing the amplitude of MEPs if that action is attributed to another individual but reduces cortico-spinal excitability when the action is illusorily attributed to the self (Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006). The ability to inhibit imitation thus requires that the individual distinguishes between internally generated motor representations consequent on the preparation of her own action and those that are triggered by observing the other person's action (Brass, Ruby, & Spengler, 2009), in a manner not unlike the proposed basis of the social Simon effect in Experiment 4. Successfully inhibiting the tendency to imitate activates cortical areas, such as the temporal-parietal junction and medial prefrontal cortex (Wang, Ramsey, &

Hamilton, 2011), which are related to perspective-taking, the sense of agency and theory of mind (Gonzalez-Liencres, Shamay-Tsoory, & Brune, 2013), as well as to discriminating between self and other (Brass, Derrfuss, & von Cramon, 2005; Brass et al., 2009; Brass & Heyes, 2005). Greater activation in medial prefrontal areas correlates with smaller congruency effects during automatic imitation, which implies better self/other distinction (Spengler et al., 2009). Furthermore, experimentally increasing self-focus, through mirror self-observation, reduces the congruency effect, by reducing RTs on incongruent trials (Spengler et al., 2010), suggesting that there may be a link with interoceptive accuracy, which is similarly enhanced by mirror self-observation (Experiment 1).

However, ‘automatic imitation’ rarely involves imitation and neither is it truly ‘automatic’ because it is not immune to interference by other processes. According to the ASL model (Catmur et al., 2009), these processes can be divided into ‘input modulation’, which alters the extent to which the relevant long-term SR bond is activated, and ‘output modulation’, where social factors inhibit the involuntary imitation (Heyes, 2011). Selective attention to one’s own actions is an example of input modulation, which reduces imitation (Bortoletto, Mattingley, & Cunnington, 2013; Chong, Cunnington, Williams, & Mattingley, 2009). It was anticipated that high interoceptive accuracy might be accompanied by heightened attention to one’s own actions. Automatic imitation can also can be reduced by modest amounts of training (Cook, Press, Dickinson, & Heyes, 2010; Gillmeister et al., 2008; Heyes, Bird, Johnson, & Haggard, 2005; Heyes & Bird, 2007), which reverses the muscle specificity of the MEPs produced by TMS (Catmur et al., 2009). Although automatic imitation is generally elicited more strongly by observation of biological than robotic action, presumably because the SR bonds are stronger (Kilner, Paulignan, & Blakemore, 2003; Liepelt & Brass, 2010; Liepelt & Prinz, 2011), training can eliminate this animacy bias (Press, Gillmeister, & Heyes, 2007).

Output modulation, by contrast, depends on the top-down influence of participants’ traits and social attitudes. For example, eye contact, or priming with pro-social cues, enhances the congruency effect (Leighton, Bird, Orsini, & Heyes, 2010; Wang & Hamilton, 2012; Wang, Newport, & Hamilton, 2011). Similarly, a desire to affiliate to the person observed increases automatic imitation in both experimental settings and social interaction (Lakin & Chartrand, 2003; Wang & Hamilton, 2012). People scoring high in 'self-monitoring' (Snyder, 1974), or who have an 'interdependent self-construal', have a greater tendency to mimic others, possibly as an unconscious affiliation strategy (Cheng & Chartrand, 2003; Obhi et al., 2011).

The ability to inhibit automatic imitation thus appears to index better self/other distinction at the level of visual and motor representation and people with high interoceptive accuracy appear more reliably able to distinguish their own bodies from those of others at a multisensory level. It was, therefore hypothesised, that in an automatic imitation paradigm, individuals with high interoceptive accuracy would successfully inhibit the tendency to imitate, whereas those with low interoceptive accuracy would exhibit less self/other distinction and would have a greater tendency to automatic imitation.

In Experiment 5, automatic imitation was assessed using the inhibition imitation paradigm developed by Brass and colleagues (Brass et al., 2005; Spengler et al., 2009). The reaction time results were compared with interoceptive accuracy, assessed by the Mental Tracking Method (Schandry, 1981). Gender, BMI, and resting heart rate were recorded, as possible confounds of the heartbeat perception task (Cameron, 2002). It was hypothesised that people who performed accurately in heartbeat perception would also be more accurate during the automatic attention task (would show a smaller congruency effect). However, both these variables might be affected by participants' general willingness and ability to attend to the tests. Attention is a possible source of input modulation in automatic imitation (Heyes, 2011). Moreover, it has also been reported that interoceptive accuracy is linked to scores on the d2 test, which measures individual differences in motivation and attention (Matthias et al., 2009). The d2 test was accordingly administered as a check for this potential confound.

4.3.2 Method

4.3.2.1 Participants

Participants were 45 students at Royal Holloway University of London who participated for course credit. All declared themselves right handed and had normal or corrected to normal vision. The data for two participants was excluded for excessive numbers of errors (more than 10%, i.e. 3SD above the mean) in the action imitation task, indicating a failure to concentrate and follow the instructions. Of the remaining 43 participants, mean age = 19.6 (SD = 4.9), nine were male. The experiment was approved by the Ethics Committee of the Psychology Department, Royal Holloway University of London.

4.3.2.2 Procedure

Participants' gender, age, height and weight were recorded. They then performed the Mental Tracking Task, followed by the test of automatic imitation and finally completed the d2 test.

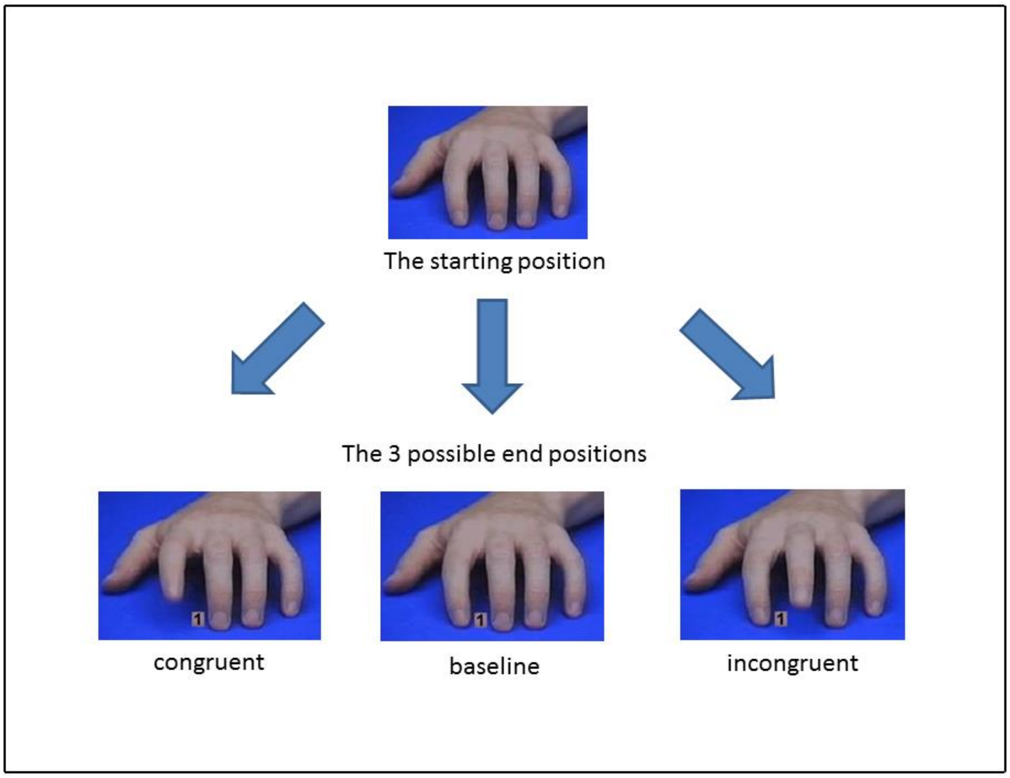
4.3.2.3 Interoceptive Accuracy and the 'Time Modulus' Measure

Interoceptive accuracy was measured with three trials of 25s, 35s and 45s, presented in random order, as described in Experiment 2 (section 2.2.2.3). Participants were also asked to estimate the length of three, randomly presented, intervals (19s, 37s, 49s, as in section 4.2.2.3) (Dunn et al., 2010).

4.3.2.4 Stimuli

The stimuli consisted of sequences of five frames kindly provided by Marcel Brass (Brass et al., 2005; Spengler et al., 2009). Each video stared with a frame showing the hand, which mirrored the right hand of the subject, in the starting position, for 2s. The next two frames, each lasting 34ms, presented a numeral (either 1 or 2) and simultaneously showed the finger movement (if any). The fourth frame showed the finger in the end position, for 1.3s, with the numeral (1 or 2) superimposed. Between trials, the screen turned black for 2.7s. Each video trial was thus 6s duration. The video hand was presented on a blue rectangular background, measuring 22 x 12cm.

Figure 4.4 Example of the Video Stimuli for the Index Finger



There were six possible video sequences, consisting of each of the two fingers (index or middle) in each of three conditions (baseline, congruent or incongruent). Participants were required to lift either the index (1) or middle (2) finger in response to a numeral appearing on the screen. The three possible conditions (for the index finger) are shown in Figure 4.3. Thus in the baseline condition, simultaneous with the appearance of the numeral, the video hand remained static. In the congruent condition the video hand lifted the finger that corresponded to the numeral shown (i.e. the index finger was lifted when the number 1 appeared). In the incongruent condition the video hand lifted the ‘wrong’ finger (i.e. the middle finger was lifted when the numeral 1 appeared).

4.3.2.5 Automatic Imitation

The stimuli were viewed on a standard PC, using Presentation software (Neurobehavioral Systems, Albany, CA). Participants were seated about 60 cm in front of the screen and were instructed to execute their movements as quickly and accurately as possible. Participants placed the index and middle fingers of their right hand on a serial response box which was linked to another PC which recorded the times of all finger movements, using Spike2 software (Cambridge Electronic

Design, Cambridge UK). This recorded the onset of the visible stimulus on screen (i.e. the numeral 1 or 2, which coincided with the onset of movement of the video hand). It also recorded whenever the participant lifted an index or middle finger. Following six practice trials, 150 experimental trials were presented in three blocks of 5mins, with obligatory rests of at least 2mins between blocks. The order of the presentation of the trials was fully randomised and comprised 25 trials in each of the six conditions.

4.3.2.6 The d2 Test of Attention

The d2 test (Brickenkamp & Zilmer, 1998) is a widely used measure of selective visual attention. The test items consist of the letters *d* and *p* with up to four dashes, arranged either individually or in pairs, above and/or below each letter. The subject is given 20s to scan across each of the 14 closely printed test lines, during which they must identify and cross out every letter *d* that has exactly two dashes, while ignoring all other distractor letters. The d2 test produces several norm-referenced scores, of which the most commonly reported are the total number of items processed (TN) regardless of whether these are correct or incorrect (this is a measure of processing speed), the percentage of errors made (E%) and the total number of items processed correctly (TN-E). This final score is designed to provide a measure of the person’s capacity to selectively orient to relevant aspects of the task, while screening out irrelevant ones.

4.3.3 Results

4.3.3.1 Data Reduction

Data for automatic imitation was extracted using Matlab (mathworks.com) and analysed with Microsoft Excel. The mean reaction time (RT) was calculated for each of the six conditions (congruent, incongruent and baseline, for each of the two fingers). The ‘congruency effect’ was calculated by subtracting the mean RT for congruent trials from the mean RT for incongruent trials.

4.3.3.2 Error Analysis

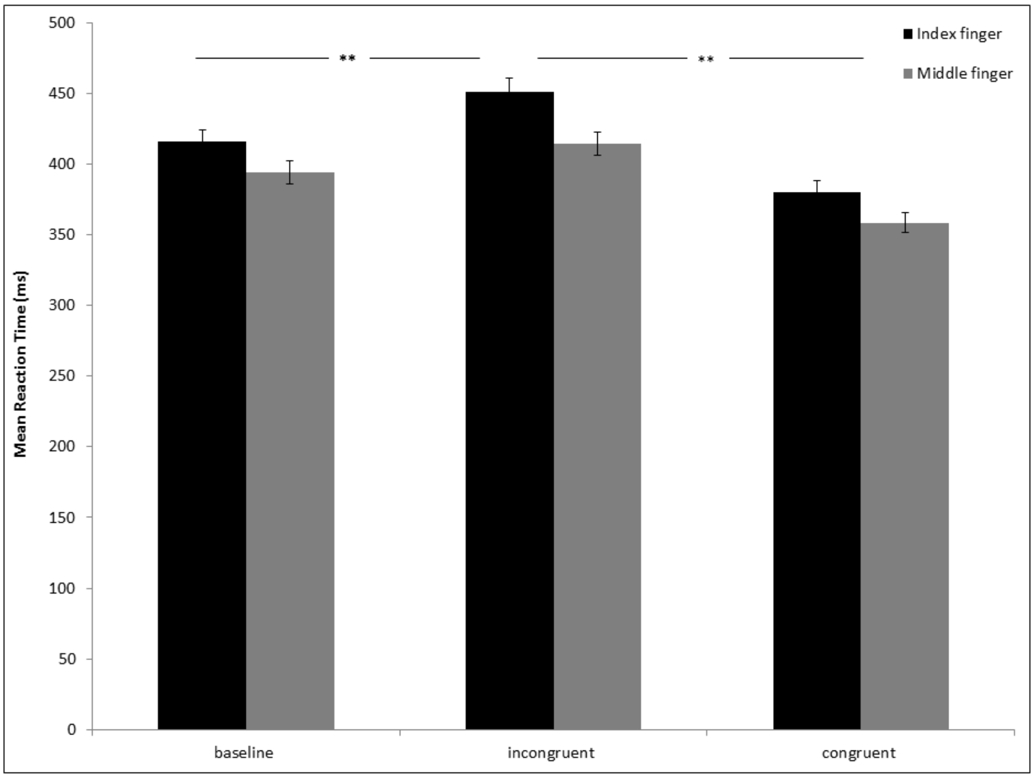
Reaction time errors were removed before analysis. There were two possible sources of errors. Firstly, participants occasionally lifted the wrong finger. Secondly, in common with most reaction time analyses, some response times were omitted as outliers (Miller & Diego, 1991). Thus RTs less than 80ms or greater than 800ms were excluded from the RT analysis (Brass et al., 2001). The rate for all errors was 2.3% of trials. Two participants were excluded for making more than 10% total errors, i.e. 3SD above the mean. The distribution of errors was thereafter approximately Normal, skewness = .64, kurtosis = -.16.

Paired sample *t* tests (with Bonferroni correction for multiple comparisons and a significance level of 0.017) showed that there were significantly more errors in the incongruent condition than in the baseline, *t*(42) = 5.07, *p* < .001, but no significant difference between the numbers of errors in the congruent condition and baseline, *t*(42) = 0.82, *p* = .42, replicating the finding of Brass et al. (2005).

4.3.3.3 Reaction Time (RT) Analysis

Repeated measures ANOVA was performed, with both the finger (index vs. middle) and the condition (congruent, incongruent and baseline) as within-subjects variables. Mauchly's test of Sphericity was significant, therefore Greenhouse Geisser corrections were applied. There was a main effect of condition (RTs in the incongruent conditions were slower), *F*(2, 84) = 186.4, *p* < .001. This indicates significant automatic imitation i.e. slower mean RTs in the incongruent than congruent condition, for both fingers (Brass et al., 2000, 2005). There was a main effect of finger, *F*(1, 42) = 13.2, *p* = .001 (reaction times were generally faster for the middle finger), as shown in Figure 4.4. The interaction of finger and condition was also significant, *F*(2, 84) = 8.9, *p* < .001. Paired samples *t* tests (with Bonferroni correction and a significance level of 0.008) showed that, compared with RTs in the baseline, RTs in the incongruent condition were significantly longer when participants were required to lift their index finger rather than their middle finger, *t*(42) = 3.32, *p* = .002. However, there was no significant difference between the two fingers for RTs in the congruent condition, compared with the baseline, *t*(42) = .57, *p* = .57. Despite the significantly shorter RTs for the middle finger, particularly in the incongruent condition, the relationships between interoceptive accuracy and the various reaction time measures in this study were very similar for the two fingers. For the remaining analysis, data for the index and middle fingers were collapsed to give a single measure of average RT in each condition.

Figure 4.5 Mean Reaction Times (RTs) by Condition and Finger (error bars represent SEM)



***significant at the 1% level*

To investigate the relationship between interoceptive accuracy and the congruency effect, the latter was calculated in the standard way (as the mean RT in the incongruent condition minus the mean RT in the congruent condition), for the average of the two fingers for each participant. Correlations between interoceptive accuracy and differences in RTs between conditions are shown in Table 4.5.

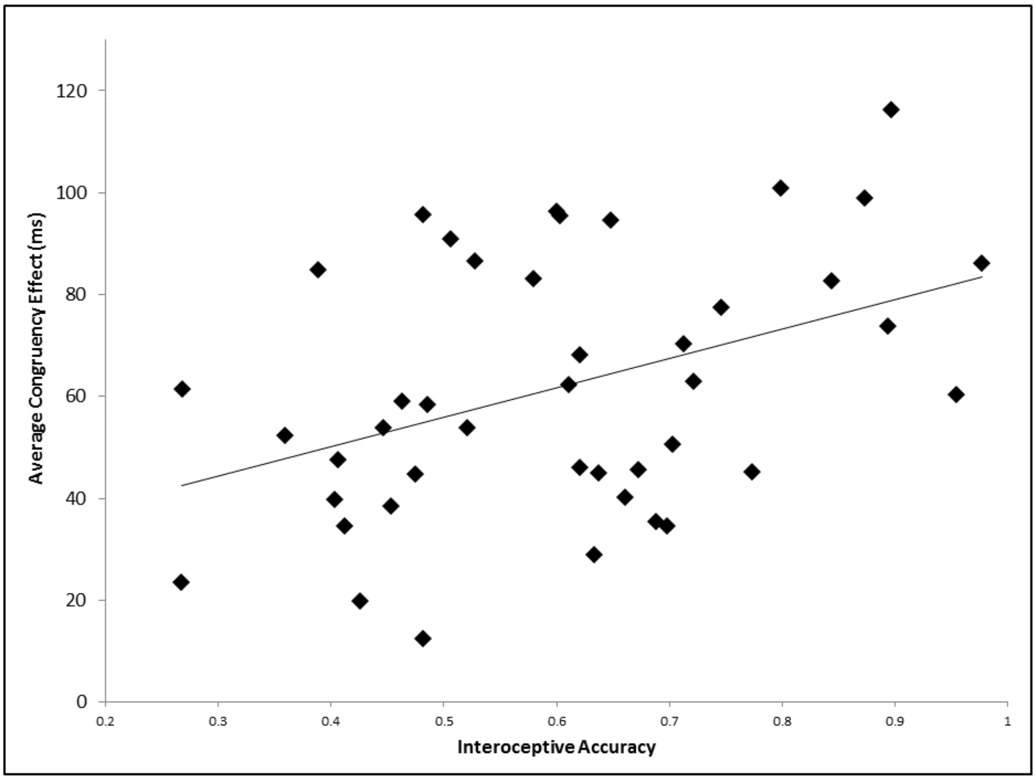
Interoceptive accuracy was positively correlated with the congruency effect (Figure 4.5) and this was wholly accounted for by RTs in the incongruent condition. Interoceptive accuracy was significantly correlated with the difference between mean RTs in the incongruent condition and the baseline but not with the difference between mean RTs in the congruent and baseline conditions.

Table 4.5 Correlations between IA and Reaction Time Measures

IA & 'the congruency effect' (mean RT in incongruent condition minus the congruent condition)	$r = .41$ $p = .006$**
IA & mean RT in the incongruent condition minus the baseline	$r = .45$ $p = .002$**
IA & mean RT in the congruent condition minus the baseline	$r = -.04$ $p = .73$

***significant at the 1% level*

Figure 4.6 Scatter Diagram of the Average Congruency Effect against Interoceptive Accuracy



The wide range of mean RTs amongst the participants (318ms - 513ms, median 398ms) might have affected the results. The percentage difference in RTs between the incongruent and congruent conditions was calculated using the formula [{(mean RT incongruent - mean RT congruent)/mean RT baseline} x 100]. This statistic was also significantly positively correlated with IA, $r = .40$, $p = .01$.

In this experiment a number of confounding variables known to impact on interoceptive accuracy were recorded which were gender, body mass index (BMI), resting heart rate, and a measure designed to assess possible guessing on the Mental Tracking Task (i.e. the ‘time modulus’ measure of the participant’s ability to estimate elapsed time). An independent samples *t* test (with equal variances not assumed) showed no effect of gender on interoceptive accuracy, $t(41) = 1.32$, $p = .24$. Likewise the correlation of interoceptive accuracy and BMI was not significant, $r = -.20$, $p = .21$. Although people with slower hearts are often better heartbeat perceivers (Cameron, 2001; Knapp-Kline & Kline, 2005), in this sample the correlation of interoceptive accuracy and average heart rate did not reach significance $r = -.22$, $p = .16$.

Given previous correlations in the literature between interoceptive accuracy and both participants’ average heart rates and the ‘time modulus’ measure (Cameron, 2002; Dunn et al., 2010), a hierarchical multiple regression analysis was performed with the average congruency effect as the dependent variable and independent variables comprising interoceptive accuracy, average heart rate, the ‘time modulus’ measure, and their interactions. The ‘time modulus’ was correlated with interoceptive accuracy, $r = .35$, $p = .02$, but only interoceptive accuracy was a significant predictor of the congruency effect (Table 4.6).

Results of the d2 test of attention were analysed in terms of the total number of items processed (TN), total number correct (TN-E) and percentage of errors (E%). Compared with published norms, d2 scores for the participants (mean TN = 516, mean (TN-E) = 493) were at the 70th percentile for students. Previous research (Matthias et al., 2009) found significant correlation between IA and TN but in this experiment none of the d2 measures was correlated with interoceptive accuracy: for TN $r = .03$, $p = .87$; for (TN-E) $r = .04$, $p = .82$; and for (E%) $r = -.02$, $p = .92$. To replicate the analysis of Matthias et al. (2009), the data was split using their cut off at IA = .85 but found no significant difference in any d2 measures between ‘good’ (IA > .85, $n = 5$) and ‘poor’ (IA < .85, $n = 38$) heartbeat perceivers (e.g. for TN, $F(1, 41) = .46$, $p = .50$)). There were likewise no significant correlations between any of the d2 measures and the average congruency effect: for TN $r = .18$, $p = .24$; for (TN-E) $r = .11$, $p = .47$; and for (E%) $r = .15$, $p = .32$.

Table 4.6 Hierarchical Multiple Regression with the Average Congruency Effect as the Dependent Variable

	Step 1	**Step 2**	**Step 3**	**Step 4**	**Step 5**	**Step 6**
Independent variables	***Beta (p)***					
Interoceptive Accuracy (IA)	1.74 (*p* = .36)	1.96 (*p* = .16)	1.90 (*p* =.16)	.52 (*p* = .14)	0.40 ** (*p* = .009)	0.41** (*p* = .006)
Average heart rate (HR)	0.22 (*p* = .82)	0.26 (*p* = .78)				
‘Time modulus’	-0.76 (*p* = .64)	-0.66 (*p* = .66)	-0.10 (*p* = .29)			
Interaction of IA & ‘time modulus’	0.19 (*p* = .86)					
Interaction of IA & HR	-1.47 (*p* = .31)	-1.55 (*p* = .25)	-1.49 (*p* = .26)	-.15 (*p* = .69)		
Interaction of ‘time modulus’ & HR	0.86 (*p* = .62)	0.85 (*p* = .62)	1.22 (*p* = .23)	.15 (*p* = .40)	.11 (*p* = .45)	
Adjusted R^2 **(*p*)**	**.08** **(*p* = .18)**	**.10** **(*p* = .11)**	**.13** **(*p* = .06)**	**.12*** **(*p* = .05)**	**.14**** **(*p* = .02)**	**.15**** **(*p* = .006)**

**significant at the 5% level* ***significant at the 1% level*

4.3.4 Discussion

The relationship between interoceptive accuracy and automatic imitation was investigated, measuring interoceptive accuracy by means of the Mental Tracking Method (Schandry, 1981) and automatic imitation by a widely used finger-lifting paradigm (Brass et al., 2005). The expected ‘congruency effect’ was obtained, i.e. mean reaction times were slower when the observed and required actions were incongruent and were faster when they were congruent (compared with the baseline of no observed movement). Interoceptive accuracy was significantly positively correlated with the congruency effect. This was fully accounted for by the difference between reaction times in the incongruent condition and the baseline. There were no significant effects of interoceptive accuracy on reaction time difference between the congruent and the baseline. The relationship observed therefore depended on reaction times the incongruent condition and thus on interference between the observed and required action (Blakemore & Frith, 2005), indicating that people with high interoceptive accuracy had greater difficulty inhibiting the tendency to automatically imitate. Had there been a motor facilitation effect it would have taken the form of shorter reaction times on congruent trials. Reaction times in the incongruent condition were significantly slower for the index finger than for the middle finger, probably because lifting an index finger is a more familiar experience than the isolated lifting of a middle finger, with a consequently stronger learned associative bond.

The results obtained were contrary to the original hypothesis. Experiments in multisensory integration have been interpreted to mean that people with high interoceptive accuracy are better at making self/other distinctions in body ownership (Tajadura-Jiménez & Tsakiris, 2013; Tsakiris et al., 2011). It had been hypothesised that this effect would translate into the motor domain. The ability to inhibit imitation is assumed to index better self/other distinction (Spengler et al., 2010) and it was therefore predicted that people with high interoceptive accuracy would more successfully inhibit the tendency to imitate. Moreover, in an identical task, Spengler and colleagues demonstrated that enhanced self-focus reduces mean reaction times on incongruent trials (Spengler et al., 2010). As Experiments 1 and 2 found, enhanced self-focus increases interoceptive accuracy. It was therefore anticipated that high interoceptive accuracy in Experiment 5 would be associated with shorter reaction times on incongruent trials and a smaller congruency effect. The results show that, on the contrary, they were *more* inclined to imitate, potentially implying greater self/other overlap.

A fundamental difference between self/other distinction in the automatic imitation task and self/other distinction in the rubber hand illusion is that, while the rubber hand illusion relies on integrating exafferent information, the confusion in the automatic imitation task is at a representational level and at a point in time before participants have any reafferent sensory information about their own movements. Automatic imitation is subject to both ‘input modulation’, by intentionally-driven changes in attention and ‘output modulation’ by inhibitory processes (Heyes, 2011). The effect in Experiment 5 was driven by slower reaction times on incongruent trials, indicating that it depended on the inhibitory effects of observing the potential sensory consequences of the action. It was therefore a result of output modulation by higher-order social processes.

A source of output modulation might be the sensitivity of people with high interoceptive accuracy to social influences, such as social anxiety or empathy. High interoceptive accuracy has been linked to anxiety (Domschke et al., 2010) and particularly to social anxiety (Terasawa et al., 2013). Trait anxiety was not assessed in this experiment but if the participants with high interoceptive accuracy were more socially anxious they might have had a greater desire to affiliate, which could have enhanced their tendency to imitate (Wang & Hamilton, 2012).

Alternatively, individual differences in empathy might have affected the results. Affective empathy has been defined as shared representations between one’s own emotional state and that of another individual, plus the ability to separate self and other (Decety & Jackson, 2004; Iacoboni, 2009; Preston & Hofelich, 2012; Zaki, Weber, Bolger, & Ochsner, 2009). People with high interoceptive accuracy are thought to experience greater empathy (Ernst, Northoff, et al., 2013; Fukushima et al., 2011) because they are assumed to have a stronger representation of the interoceptive consequences of an action, for example, they are more sensitive to masked fear conditioning (Katkin et al., 2001). Scores on the Empathic Concern scale of the Interpersonal Reactivity Index (Davis, 1983) correlate with the amplitude of heartbeat evoked potentials (Fukushima et al., 2011), which are larger in people with high interoceptive accuracy (Pollatos & Schandry, 2004). Empathy has, in turn, been linked to action observation. People trained to inhibit imitation subsequently perform better on a perspective taking task (Santiesteban et al., 2012). Moreover, when participants observe another individual reaching for a cup, inferior frontal mirror activity is greater in those people who have higher scores on the Empathic Concern subscale (Kaplan & Iacoboni, 2006). Such motor activity in response to action observation is linked to a greater tendency to imitate (Catmur, Walsh, & Heyes, 2007; Obhi et al., 2011; Schütz-Bosbach et al., 2006). Empathy is inversely correlated with narcissism (Raskin & Terry, 1988) and it has recently been shown that individuals who are high in trait narcissism - thus displaying a lack of empathy and concern for others - have a greater ability to inhibit automatic imitation (Obhi, Hogeveen, Giacomin, & Jordan, 2013). Potentially, high interoceptive accuracy might have involved stronger interoceptive representations of the consequences of an action, implying higher empathy, greater mirror neuron activity in response to observed action and hence a greater tendency to imitate. However, these links are indirect and speculative. A direct link between interoceptive accuracy and empathy has yet to be established.

A final possibility is that good heartbeat perceivers may be more averse to making errors. A recent novel EEG study by Sueyoshi and colleagues reports that performance of the Mental Tracking Method correlates with post-error slowing in reaction times on the Simon task, as well as with the amplitude of the error-positivity, which is a late component of the neural response to making an error (Sueyoshi et al., 2014). While the meaning of the error positivity is not fully understood, it is thought to reflect awareness of making a mistake (Endrass, Reuter, & Kathmann, 2007). Its amplitude is modulated by the salience of the error (Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010) and the signal originates in anterior cingulate cortex (van Veen & Carter, 2006), which is generally coactive with the anterior insula (Craig, 2009). Activity in the anterior insula is closely linked to the autonomic responses that occur when a person is aware of having made an error, (Ullsperger et al., 2010), which reflects the insula's role in risk monitoring (Preuschoff, Quartz, & Bossaerts, 2008). Moreover, a study by Band and colleagues suggests that it is not necessary to make an error in order to experience error related responses. They found that error-related potentials are evoked by action effects that violate expectations, even when these are task-irrelevant (Band, van Steenbergen, Ridderinkhof, Falkenstein, & Hommel, 2009).

Taken together, these results may be explained if people with high interoceptive accuracy experience stronger negative affect and greater autonomic reactivity when they are aware of having made a mistake. The amplitude of the error-positivity correlates with the Personal Distress subscale of the Interpersonal Reactivity Index (Davis, 1983) (Larson et al., 2010), which similarly implies a heightened aversive response. If good heartbeat perceivers experience higher salience of errors and greater negative affect, as well as greater insula and anterior cingulate activity when making errors, then avoiding errors during automatic imitation could lead to more insula engagement and greater response conflict, which would slow their reactions.

Experiment 5 had several limitations. Trait variables such as empathy and social anxiety were not measured, which might have been a source of output modulation that could mediate between interoceptive accuracy and imitation inhibition. Automatic imitation using finger-lifting paradigms is open to the criticism that the effect is at least partially driven by spatial compatibility (Cooper, Catmur, & Heyes, 2012), although an elegant experiment has shown that automatic imitation persists even when the observed hand is flipped, such that the spatial aspect of the movement is no longer driving the effect (Brass et al., 2001). The results presented here might be explained if people with high interoceptive accuracy have greater susceptible to spatial compatibility effects, however, no such effect was observed in Experiment 4, using the Simon effect.

4.3.5 Conclusion

Interoceptive accuracy modulates self/other distinction in multisensory contexts. Here it was demonstrated for the first time that interoceptive accuracy also impacts on shared representations in the motor domain, such that people with high interoceptive accuracy have greater difficulty in inhibiting the tendency to imitate, in a standard automatic imitation paradigm. The result, however, was concentrated in incongruent trials, indicating that it is the result of output modulation, through some unidentified top-down social effect and was not due to the influence of interoception on the representation of the action.

Chapter 5. 'The Acting Self': Interoceptive Accuracy and the Sense of Agency.

5.1 Experiment 6. Interoceptive Accuracy and Intentional Binding

5.1.1 Introduction

In Experiments 4 and 5 the participant's action was cued. Experiment 6, by contrast, investigated the effect of interoceptive accuracy during voluntary action, examining whether interoceptive accuracy modulates the sense of agency (Moore & Obhi, 2012). Agency is an essential component of models of the self, suggesting a possible link with interoception. Damasio, for example, proposes that the sense of agency emerges when the 'core self' is engaged with objects (Damasio, 2010), while Gallagher defines a 'minimal self' as comprising feelings of body ownership and the sense that we are the agents of our own actions (Gallagher, 2000). Abnormalities in the sense of agency compromise the integrity of the self, for example, in delusions of control (Blakemore et al., 2002). In Experiment 6, the sense of agency was measured by 'intentional binding' (Haggard, Clark, & Kalogeras, 2002), using the classic Libet clock paradigm (Libet et al., 1983).

Within the contexts of Experiments 4 and 5, no evidence was found linking interoceptive accuracy to action. In Experiment 4 there was no effect of interoceptive accuracy on the participant's tendency to form a mental representation of the partner's action during the social Simon task. In Experiment 5 interoceptive accuracy was linked to output modulation during automatic imitation but there was no effect on input modulation, suggesting that interoceptive accuracy did not affect the preparation of, or attention to, the action. An important strength of the intentional binding paradigm, however, is that this method allows separate analysis of the potential effect of interoceptive accuracy on the preparation of an action and on the sensory consequences of that action. Moreover, it provides both behavioural and EEG measures with which to assess these potential influences.

Agency depends on the intention to act, as well as execution of the action, and thus relies on efferent motor representations combined with reafferent sensory feedback (Tsakiris & Haggard, 2005). According to both the Theory of Event Coding

(Hommel, 2009) and predictive coding accounts of action (Adams et al., 2012), movements are represented in terms of their sensory consequences. The influential comparator model of motor control (Blakemore et al., 2002; Frith, 2012) proposes that feelings of agency arise when there is a match between the predicted consequences of a movement and the sensory feedback. However, agency has also been characterised as *post hoc* confabulation, resulting from our intentions to act (Wegner, 2003). A synthesis of these ideas proposes that agency depends on a combination of predictive processes that precede the performance of an action as well as postdictive (reconstructive) processes, such as top-down modulation by context and prior assumptions (Moore & Haggard, 2008; Moore, Wegner, & Haggard, 2009). In the light of research showing the influence of both bottom-up and top-down cues (Moore & Obhi, 2012), the comparator conceptualisation has consequently been extended into the 'multifactorial weighting account' of agency (Synofzik, Vosgerau, & Newen, 2008a). In the multifactorial account, agency depends on the optimal integration of all the available sensory and motor cues that are associated with the given movement (Moore & Fletcher, 2012; Synofzik, Vosgerau, & Newen, 2008a). This fits well with predictive coding accounts, in which the brain weighs the various sources of incoming sensorimotor data according to their 'precision' (reliability) and arrives at a prediction (a best guess), for example, that the most probable cause of all the available data is that 'I did that!' (Wolpe & Rowe, 2014).

Interoception has, until recently, been neglected within the multifactorial model. Emotion however, contributes to the representation of actions (Eder, Müsseler, & Hommel, 2012) and all affect depends on interoception (Gentsch & Synofzik, 2014). Seth and colleagues place affect and agency at the heart of self-awareness, proposing that the sense of agency depends on the integration of interoceptive/affective and exteroceptive sensory signals (Seth et al., 2011). In a rare reference to individual differences in interoceptive accuracy, these authors suggest that people with high interoceptive accuracy are those who potentially put more weight on interoceptive signals, when integrating cues in an optimal manner, while individuals with relatively low interoceptive accuracy may rely preferentially on exteroceptive sensory signals (Seth et al., 2011). If this is a correct interpretation of individual differences in interoceptive accuracy, it suggests that interoceptive accuracy is likely to modulate the sense of agency.

Experiment 6 therefore had a dual purpose. Primarily the aim was to investigate whether interoceptive accuracy affects the sense of agency. Equally importantly, however, the paradigm allows both EEG and behavioural analysis that can discriminate whether interoceptive accuracy affects the preparation of an action and/or influences the sensory consequences of that action.

‘Intentional binding’ (Haggard et al., 2002) provides an objective and reliable measure for probing the implicit sense of agency (Moore & Obhi, 2012). When people make voluntary actions that cause sensory outcomes, they judge the timing of their movements as later than they really occur (‘action binding’) and they perceive the sensory consequences of their actions as happening earlier (‘effect binding’) (Moore & Haggard, 2008). Action binding and effect binding together make up intentional binding but they rely on dissociable processes (Waszak, Cardoso-Leite, & Hughes, 2012; Wolpe, Haggard, Siebner, & Rowe, 2013). For example, theta burst TMS stimulation over the pre-supplementary motor area (pre-SMA) disrupts effect binding but not action binding (Moore, Ruge, Wenke, Rothwell, & Haggard, 2010). Similarly, effect binding but not action binding is influenced by causal beliefs about the authorship of a sound (Desantis, Roussel, & Waszak, 2011).

For intentional binding to occur there must be both an intentional actor and a causal relationship between action and outcome (Haggard, Poonian, & Walsh, 2009; Moore & Obhi, 2012). Consequently, factors that impact on intentional binding include learned action-effect associations, as well as beliefs about causal factors (Desantis, Roussel, & Waszak, 2011; Haggard & Cole, 2007; Haggard et al., 2009; Moore et al., 2010). An observer will, for example, bind the actions of another individual on the assumption that the person is an intentional agent (Poonian & Cunnington, 2013) but they may also bind the actions of a computer on the basis of learned causality (Buehner & Humphreys, 2009). Importantly, emotion has been shown to affect intentional binding, which is stronger for positive rather than negatively valenced outcomes (Yoshie & Haggard, 2013) and is likewise stronger when the action is associated with a monetary reward (Takahata et al., 2012). Intriguingly, there are considerable inter-individual differences in intentional binding (Wolpe et al., 2013), the sources of which have not yet been established (Haggard & Cole, 2007; Moore & Obhi, 2012). Potentially interoceptive accuracy may be a contributing factor.

In accordance with Libet's classic paradigm (Libet et al., 1983), Experiment 6 included EEG recording while participants made spontaneous button presses and heard sounds. This allows analysis of the readiness potential, which is a slow negative deflection observed over frontocentral electrodes when people prepare an action. The paradigm also enables analysis of the auditory-evoked potentials, which are produced by a tone generated either at random by the computer, or as a result of the participant's action.

The readiness potential (RP) produced during the preparation of a voluntary action can be divided into two parts. These are the 'early readiness potential', originating in the pre-SMA, which lasts from about 2sec to 500ms before the movement onset, and a steeper 'late readiness potential', from 500ms to action onset, with origins in primary motor cortex and lateral premotor cortex (Shibasaki & Hallett, 2006). The amplitude of the late readiness potential depends on motor factors such as the speed, precision and the complexity of the action (Shibasaki & Hallett, 2006). By contrast, the amplitude of the early readiness potential has recently been shown to correlate with effect binding (Jo, Wittmann, Hinterberger, & Schmidt, 2014). Moreover, belief in free will, which presumably affects the sense of agency, modulates the amplitude of the early readiness potential (Rigoni, Kühn, Sartori, & Brass, 2011). In Experiments 4 and 5 no link was identified between interoceptive accuracy and preparation of action. However, the paradigm in Experiment 6 allowed this to be examined more closely. If a relationship were to exist between interoceptive accuracy and action, then this should be reflected in the behavioural measure of action binding and also perhaps in the amplitude of the late readiness potential in EEG.

An additional test of the possible effects on interoceptive accuracy on the preparation of action is provided by the paradigm. Libet famously showed that although the readiness potential can be observed up to 2.5sec before the onset of movement, people only become aware of their 'urge' to move (known as the W judgment) about 200ms before making a key press (Libet et al., 1983). It is not necessary to ask participants for the W judgment in order to calculate intentional binding, however, the urge to move is linked to the time at which a motor plan is specified (Haggard & Eimer, 1999; Wolpe & Rowe, 2014). Moreover, attention to the intention to move (i.e. to W) is associated with increased activity in the pre-SMA, which is the source of the early readiness potential (Lau, Rogers, & Passingham, 2006). The participant's judgment of when they moved (M) and their sense of when they felt the urge to move (W) are dissociable and they activate different neural circuits (Lau, Rogers, Ramnani, & Passingham, 2004). For example, the W but not M judgment is disrupted in Tourette's syndrome (Moretto, Schwingenschuh, Katschnig, Bhatia, & Haggard, 2011). Given that interoceptive accuracy measures an individual's consciousness of internal bodily signals, it has been suggested that a person with high interoceptive accuracy might have earlier access to awareness of their own actions and might therefore report earlier W judgments (Penton, Thierry, & Davis, 2014).

In the light of the results of Experiments 4 and 5, which showed no relationship between interoceptive accuracy and action, it was hypothesised that interoceptive accuracy would not modulate action binding. However, interoceptive accuracy may be characterised as an individual's tendency to attend preferentially to interoceptive signals (Herbert & Pollatos, 2012; Seth et al., 2011). This could imply that heartbeat perception will impact on effect binding. The resistance of people with high interoceptive accuracy to the rubber hand illusion (Tsakiris et al., 2011), has been interpreted as implying stronger feelings of body ownership and better ability to distinguish self from other, which might imply that they also feel a stronger sense of agency.

A further advantage of the Libet paradigm is that sensory attenuation can be observed between the amplitude of the auditory-evoked potential for a randomly generated tone and the comparable evoked potential when the sound is produced by the participant's own actions (Hughes, Desantis, & Waszak, 2013; Roussel, Hughes, & Waszak, 2013). Sensory attenuation is an essential aspect of self-generated action (Blakemore, Wolpert, & Frith, 2000; Shergill, Bays, Frith, & Wolpert, 2003) and is itself an indication that the individual is the author of the action. It has been proposed as an alternative measure of feelings of agency (Wolpe & Rowe, 2014). There are various theoretical explanations for sensory attenuation (Blakemore et al., 2002; Brown, Adams, Parees, Edwards, & Friston, 2013; Wolpe & Rowe, 2014) but all rely on the expected sensory consequences of the action. Sensory attenuation can be studied within the Libet paradigm as the difference in amplitude of the auditory-evoked potential between self-generated and computer-generated tones. If interoceptive accuracy reflects the tendency to attend to interoceptive rather than exteroceptive consequences of an action, then sensory attenuation might be modulated by heartbeat perception.

In Experiment 6 all participants performed the classic Libet clock experiment in six blocked conditions under EEG. They reported the time at which they had heard a computer-generated tone (the S judgment) or they made freely chosen, spontaneous button presses and reported either the time at which they had 'felt the urge to move' (the W judgment), or when they had made the button press (M judgment). In three further operant conditions (SO, WO and MO), similar judgments were required but now the participant's button press caused an auditory tone. Intentional binding was calculated as the sum of action binding (the perceived shift in the timing of the movement towards the tone it causes) and effect binding (a perceived shift in the timing of the tone towards the action that created it) (Haggard et al., 2002). The amplitude of readiness potentials in all five conditions that involved movement were analysed, as well as the amplitude of auditory-evoked potentials in the conditions involving sound.

There were six hypotheses. (i) It was anticipated that individual differences in the behavioural measures of agency (indexed by intentional binding) would be associated with individual differences in interoceptive accuracy. However, given that higher interoceptive accuracy does not appear to be associated with awareness of action in Experiments 4 and 5, it was expected that interoceptive accuracy would modulate effect binding but not action binding. (ii) It was similarly hypothesised that interoceptive accuracy would not be related to the amplitude of the readiness potentials in any condition; and moreover, (iii) that interoceptive accuracy would not correlate with behavioural measures of the conscious awareness of the urge to move (the W judgment). (iv) Following the results of Jo et al. (2014), it was anticipated that effect binding would correlate with the amplitude of the early readiness potential. (v) Given that they are both measures of agency (Wolpe & Rowe, 2014), it was anticipated that effect binding would correlate with sensory attenuation, measured as the difference in amplitude between the auditory-evoked potential in the condition in which a tone was computer-generated (S) and the operant condition in which it was self-generated (SO). (vi) From the hypothesis that interoceptive accuracy would be linked to effect binding, it was further anticipated that interoceptive accuracy would correlate with sensory attenuation. Moreover, if people with high interoceptive accuracy attend preferentially to the interoceptive rather than the exteroceptive consequences of their actions, then it was expected that this correlation would be accounted for by a relationship between interoceptive accuracy and lower amplitude of the auditory-evoked potential in the SO condition.

5.1.2 Methods

5.1.2.1 Participants

30 students (4 men) at Royal Holloway University of London took part for payment. All declared themselves right handed and used their right hand for key presses. Due to technical failure, data for one participant was lost in all three operant conditions and this individual was necessarily excluded. Data for a single participant who showed neither effect binding nor action binding was also excluded (following Jo et al., 2014). One participant recorded no data in the operant movement condition (MO) but data for the other five conditions was available and was included in the analysis wherever possible. There were therefore 28 participants (4 men), mean age 20.3 years (SD = 3.0). The experiment was approved by the Ethics Committee of the Psychology Department, Royal Holloway University of London.

5.1.2.2 Procedure

Participants reported their gender, age, height and weight. They then performed the Mental Tracking Task, including the time modulus measure and finally completed the Libet experiment in all six conditions.

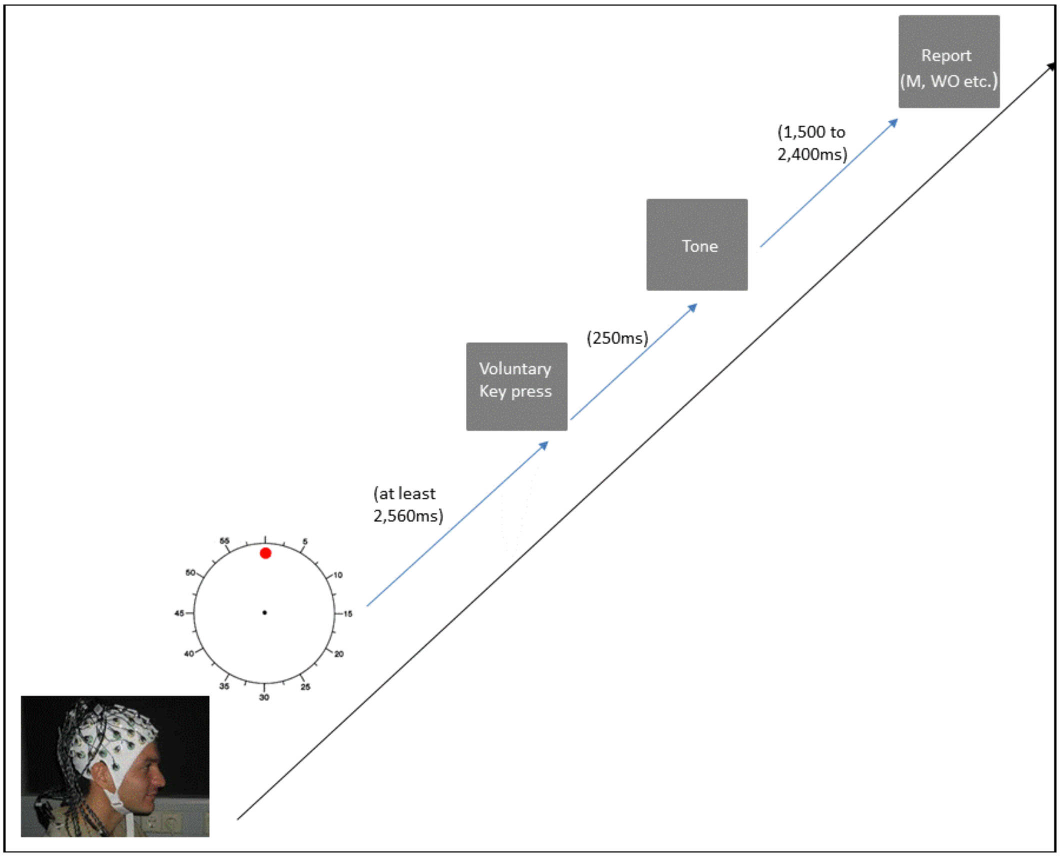
5.1.2.3 Interoceptive Accuracy

Interoceptive accuracy was measured as in Experiment 1 (section 2.2.2.3). The participant’s ability to estimate elapsed time was assessed by the ‘time modulus’ measure, as described in Experiments 4 and 5 (section 4.2.2.3).

5.1.2.4 Libet Paradigm

The EEG experiment followed Libet’s classic paradigm (Libet et al., 1983). Stimuli were displayed on a standard PC, using Presentation software (Neurobehavioral Systems, Albany, CA). Participants sat at a distance of 50cm from the monitor, on which was displayed a white clock face, 13cm in diameter, marked from 5 to 60, in units of 5. A red dot rotated clockwise round the clock face, completing one rotation every 2,560ms. Participants were instructed to allow the dot to make at least one full rotation before making a voluntary and spontaneous key press, at a freely chosen time. The dot continued to rotate for a random period between 1.5s and 2.4s following the key press (Figure 5.1). After each trial, participants were prompted by the computer to make timing judgments. There were six conditions, each consisting of 40 trials, presented in blocks. The order of presentation of the conditions was counterbalanced. In the sound condition (S) the participants were instructed not to make any movement but to report when they had heard a computer-generated sound that occurred at a random interval between 2.5s and 8s after the start of the trial. In the other five conditions participants made a spontaneous key press at a time of their own choosing. In the movement condition (M) they reported the time on the clock face at which they judged that they had made the freely chosen action. In the W condition they reported when they had first ‘felt the urge to move’. In each of three further operant conditions the computer generated a tone 250ms after the key press. In the operant movement condition (MO) participants were asked to report when they had made the spontaneous key press; in the operant ‘urge’ condition (WO) when they had first ‘felt the urge to move’; and in the operant sound condition (SO) when they had heard the sound that had been caused by their key press (Table 5.1).

Figure 5.1 Schematic Depiction of a Single Libet Trial



EEG activity was recorded using Ag/AgCl electrodes, fixed with a head cap and electrolyte gel (BioSemi Active Two system). Impedance was kept below 5kΩ and the sampling rate was 512Hz. 64 electrodes were arranged using the 10/20 system, with a further 7 external electrodes (two were attached to the ear lobes, two recorded vertical and two horizontal eyes movement, one was placed on the left chest to provide heartbeat data).

The EEG data was analysed using Brain Vision Analyzer software (Brain Products, Munich, Germany). Data was downsampled to 250Hz and re-reference to linked earlobes. Filters of 70Hz and 0.01Hz were applied. To analyse readiness potentials, data was segmented into epochs of -2500ms to +500ms, with respect to the key press. A baseline of 200ms (-2500ms to -2300ms) was applied. Artefact rejection was performed semi-automatically. The maximum voltage change allowed was 80µv/ms, with lowest allowable activity 0.5µv. All epochs were visually inspected for movement artefacts and for trials in which participants made key presses without allowing a full rotation of the clock, so that a full readiness potential could not be recorded. No artefact correction was applied. 25% of trials were rejected, of which 9% were for not obeying the instructions and 16% for movement artefacts.

In order to compare auditory-evoked potentials for the sound (S) and operant sound conditions (SO), an epoch of -100ms to +500ms was selected, with a baseline of -100ms to sound onset (Figure 5.1). Filters and artefact rejection were applied as above. 14% of trials were rejected for movement artefacts.

5.1.3 Results

Behavioural Data

5.1.3.1 Interoceptive Accuracy

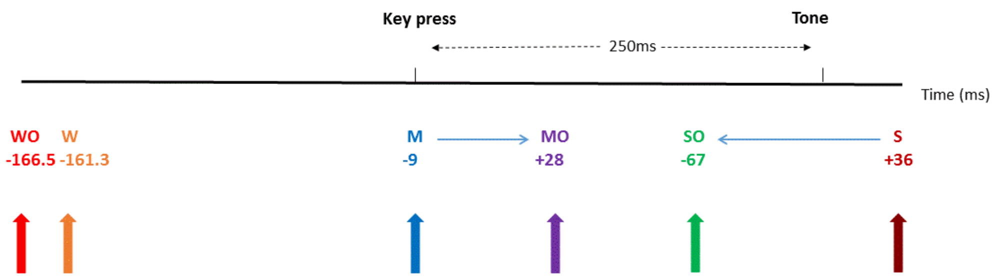
Interoceptive accuracy (IA) was calculated in the standard manner (section 2.2.2.4). Mean IA = .63, SD = .16 (median = .61). The time modulus measure of accuracy in estimating elapsed time was calculated similarly (section 4.2.2.3).

5.1.3.2 Intentional Binding

A repeated measures ANOVA was performed on the mean timing judgments (Table 5.1). The nature of the timing judgement (urge to move, actual movement, or perception of the sound) and whether the condition was operant vs. non-operant were within-subjects variables. Mauchley's test of Sphericity was significant, so Greenhouse Geisser corrections were applied. There was a main effect of judgment, $F(2, 52) = 25.20$, $p < .001$, $\eta^2 = .49$; and a main effect of whether the condition was operant or non-operant, $F(1, 26) = 6.57$, $p = .02$, $\eta^2 = .20$; as well as an interaction, $F(2, 52) = 20.99$, $p < .001$, $\eta^2 = .45$. Paired samples t tests showed that the judgement of the timing of the sound differed significantly between the operant and non-operant conditions (S and SO), $t(27) = 6.68$, $p < .001$. Similarly, the judgment of movement differed significantly between non-operant and operant conditions (M and MO), $t(26) = 2.43$, $p = .02$, indicating, respectively, significant effect binding and significant action binding. There was no significant difference between the W and WO judgements, $t(27) = 0.34$, $p =.74$.

Intentional binding (Haggard et al., 2002) was calculated for each participant, from mean timing judgments, as the sum of effect binding (S - SO), whereby the sound was perceived as closer to the button press in the operant condition, and action binding (MO - M), whereby the participant perceived the time of movement as closer to the sound in the operant condition. No outliers were excluded. Times for M, W, MO and WO were calculated with respect to the key press. Times for S and SO were measured with respect to the onset of sound. Negative values indicate that the judgment of time was in advance of the key press or the onset of the tone.

Figure 5.2 Diagrammatic Representation of the Mean Results for the Six Measures



MO - M (action binding) is a shift in the judgment of the timing of the key press towards the tone.

S - SO (effect binding) is a shift in the judgment of the timing of the sound towards the action.

Intentional binding = (MO - M) + (S - SO)

The results indicated that intentional binding was driven by effect binding (Figure 5.2 and Table 5.1). Two participants exhibited no effect binding, while eleven showed no action binding. Applying a less stringent criterion than Jo et al. (2014), who excluded all those participants demonstrating no effect binding, in this experiment the single participant who exhibited neither effect binding nor action binding was omitted from the analysis.

Table 5.1 Descriptive Statistics for Mean Judgment of Timing in each Condition and for Mean Effect Binding and Intentional Binding

Measure	**Judgment required from the participant**	**Mean (ms)**	**SD**
M	No sound. Report when you pressed the key.	-12.9	51.2
W	No sound. Report when you felt the urge to move	-161.3	156.1
S	No key press. Report when you heard the computer-generated sound	28.6	73.6
MO	Sound generated by the key press. Report when you pressed the key.	18.6	78.2
WO	Sound generated by the key press. Report when you felt the urge to move.	-166.5	178.6
SO	Sound generated by the key press. Report when you heard the sound.	-87.9	85.5
Effect binding	S - SO	116.5	90.2
Action binding	MO - M	29.7	61.4
Intentional binding	(MO – M) + (S –SO)	138.5	102.0

Interoceptive accuracy was significantly correlated with intentional binding (Table 5.2), which was wholly accounted for by the correlation between interoceptive accuracy and effect binding. (Figure 5.3). Power was calculated, post hoc, for the given parameters, which are n = 28, and r = .39, α = .05, using a statistical table (www.statstodo.com/SSizCorr_Pgm.php), which indicated that the experiment was somewhat underpowered (power = .68). A sample size of 39 would be necessary for the generally recommended level of power of .8.

Hypothesis (i) was thus confirmed. Interoceptive accuracy was correlated with effect binding. In the operant sound condition, the higher their interoceptive accuracy, the closer participants perceived the self-generated sound to the key press that had caused it. There was no relationship between interoceptive accuracy and action binding, *r* = -.01, *p* = .95. Interoceptive accuracy was not correlated with the judgment of timing in any other condition, *p* > .58. Confirming hypothesis (iii), interoceptive accuracy was not related to the timing at which individuals reported their awareness of the urge to move: for W, *r* = -.07, *p* = .71; and for WO, *r* = .08, *p* = .70. Because a fundamental hypothesis of Experiment 6 was that interoceptive accuracy and effect binding would be correlated and that there would be no correlation between interoceptive accuracy and any other behavioural measure, no correction was made for multiple comparisons.

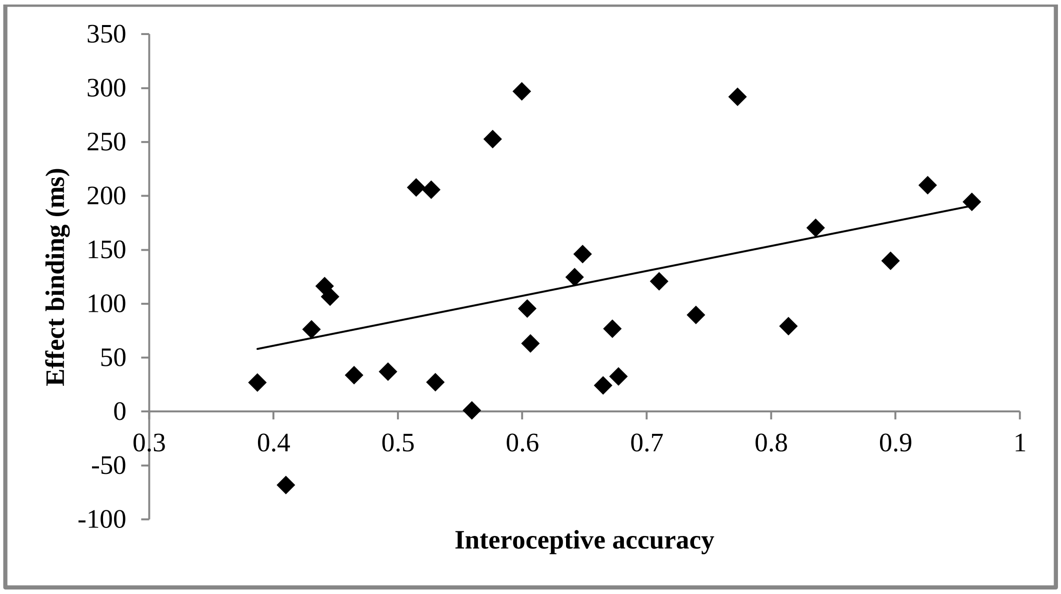
Table 5.2 Correlations between Interoceptive Accuracy and the Behavioural Measures

M *r* = -.11 *p* = .60	MO *r* = -.11 *p* =.71	MO - M (action binding) *r* = -.01 *p* = .95	Intentional binding *r* = .39 *p* = .04*
S *r* = .05 *p* =.79	SO *r* = -.36 *p* = .06†	S – SO (effect binding) *r* = .42 *p* = .03*	
W *r* = -.07 *p* = .71	WO *r* = .08 *p* = .70	WO – W r = .23 *p* = .25	

***significant at the 5% level**

†significant at the 10% level

Figure 5.3 Scatter Diagram Showing the Correlation of Interoceptive Accuracy and Effect Binding



The time modulus measure (of participants' ability to estimate the length of an elapsed interval) was correlated with interoceptive accuracy, *r* = .39, *p* = .04. To check for potential confounding effects, the time modulus measure, as well as the participant's resting heart rate, were added as regressors into a multiple regression with effect binding as the dependent variable. Interoceptive accuracy was the sole significant predictor of effect binding. These results indicate that participants' ability to estimate elapsed time and their true resting heart rates were not significant confounds in this experiment.

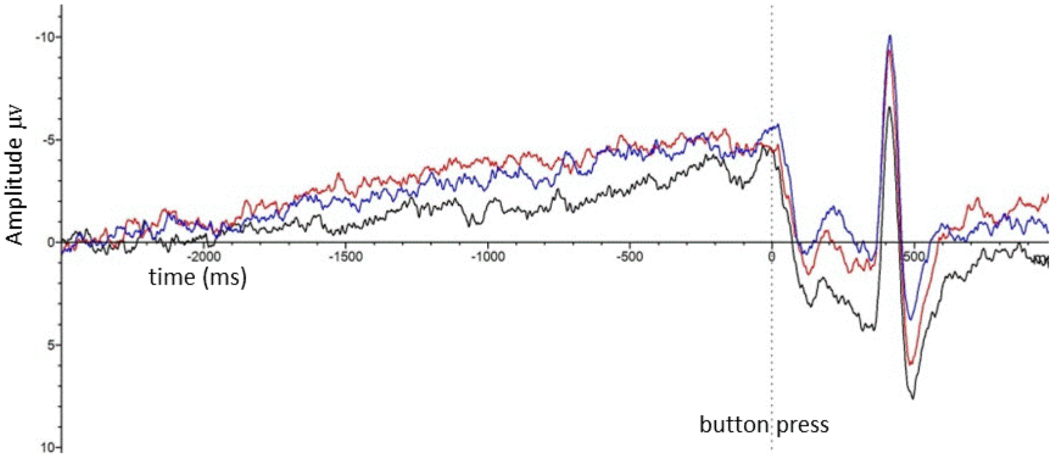
EEG Data

5.1.3.3 Readiness Potentials

Readiness potentials were analysed as the average activity at the 9 frontocentral electrodes where activity was greatest during the trial epoch of -2500ms to +500ms (FC1, FCz, FC2, C1, Cz, C2, Cp1, CPz, CP2) (Figures 5.2 and 5.3).

In the sound condition S, where the participants did not move but simply reported when they had heard a tone, the amplitude of the whole negative deflection, in the interval -2,300ms to the key press, did not differ significantly from zero, *t*(27) = 0.48, *p* = .63, confirming that, in the absence of movement, there was no readiness potential.

Figure 5.4Readiness Potential, at Cz, for the Operant Conditions MO (black), WO (red), SO (blue), Grand Averages



To compare the amplitudes of the readiness potentials in the other five conditions, which did involve movement, the readiness potential was split into an early RP component, from -2300 to -800ms, and a late RP, from -500ms to movement onset (Jo et al., 2014; Shibasaki & Hallett, 2006). Repeated measure ANOVA on the amplitudes of the PRs with early vs. late RP and condition (M, W, MO, WO, SO) as within-subjects variables, showed no main effect of condition $F(4, 100) = 1.45$, $p = .22$ and no interaction of early vs. late RP with conditions, $F(4, 100) = 0.57$, $p = .67$. There was the expected main effect of early vs. late RP, as the readiness potential naturally increases in amplitude over its time course, $F(1, 100) = 46.4$, $p < .001$ (Figure 5.2).

In the operant sound condition SO, the correlation was significant between mean effect binding for a given individual and mean amplitude of the early RP for that participant, $r = -.40$, $p = .04$. However, a similar correlation of effect binding and the amplitude of the late RP in SO was not significant, $r = -.29$, $p = .14$, confirming hypothesis (iv) and replicating the results of Jo et al. (2014). -In this experiment but not in Jo et al., there was a significant relationship between effect binding and the amplitude of the whole RP, $r = -.42$, $p = .03$. Effect binding was not correlated with the amplitude of the early or late RP in any other experimental condition, $p > .51$.

Interoceptive accuracy was not correlated with the amplitude of the early or late RP in either condition M or MO, $p > .66$, therefore hypothesis (ii) was confirmed.

Interoceptive accuracy did not affect the preparation of action. Moreover, interoceptive accuracy was not correlated with the amplitude of the early or the late RP in either condition W or condition WO, $p > .43$, further confirming hypothesis (iii) that there was no relationship between interoceptive accuracy and the W judgment. Interoceptive accuracy was not correlated with the amplitude of the early or late RP in condition SO, $p > .60$.

5.1.3.4 Auditory-evoked Potentials

Taking the average amplitude of the same 9 electrodes (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2), the N1 component of the auditory-evoked potential, was visible in the interval 100-200ms, peaking around 155ms (Figures 5.3 and 5.4).

The grand averages for auditory-evoked potentials for the sound condition S and the operant sound condition SO were compared (Figure 5.4). Comparison of the latency of the peak of N1 for the grand averages, showed that N1 peaked significantly earlier in the operant sound condition SO, $t(27) = 4.1$, $p < .001$, (Wolpe et al., 2013).

Figure 5.5 Comparison of the Scalp Distribution of Auditory-Evoked Potentials, at Cz, for Conditions S and SO, from Grand Averages

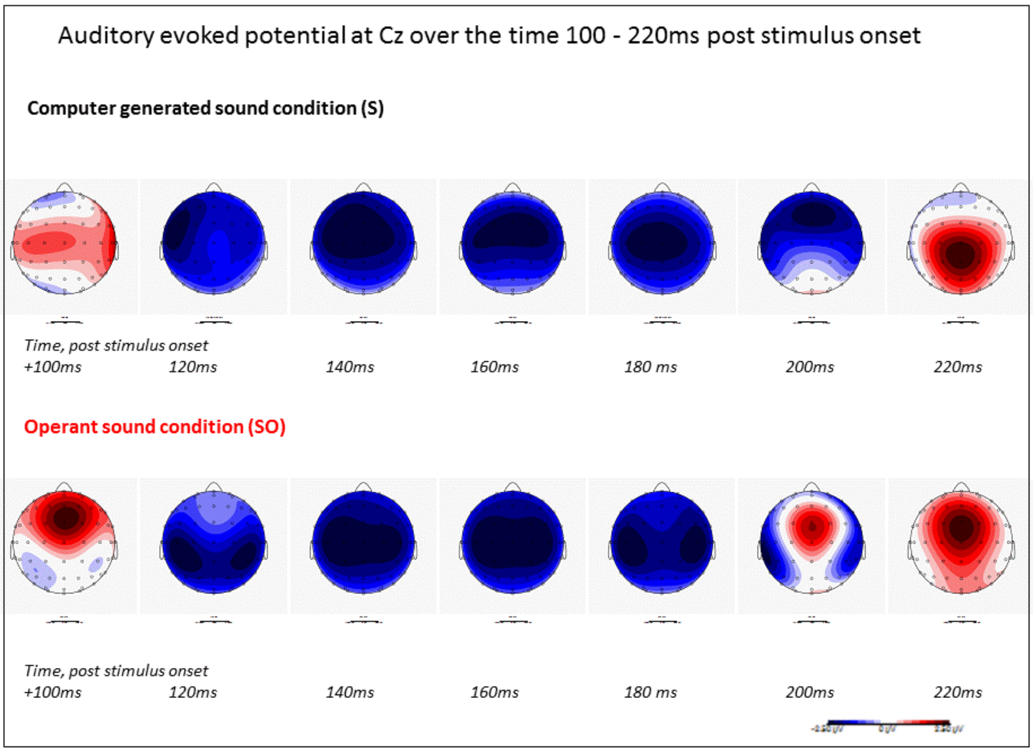
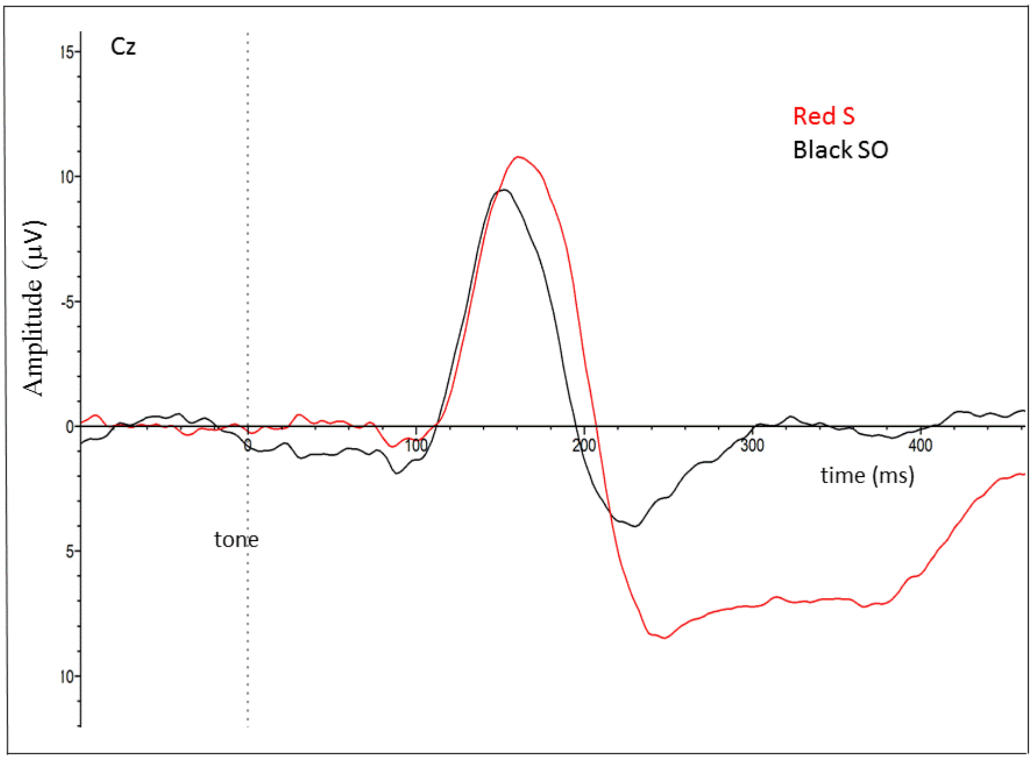


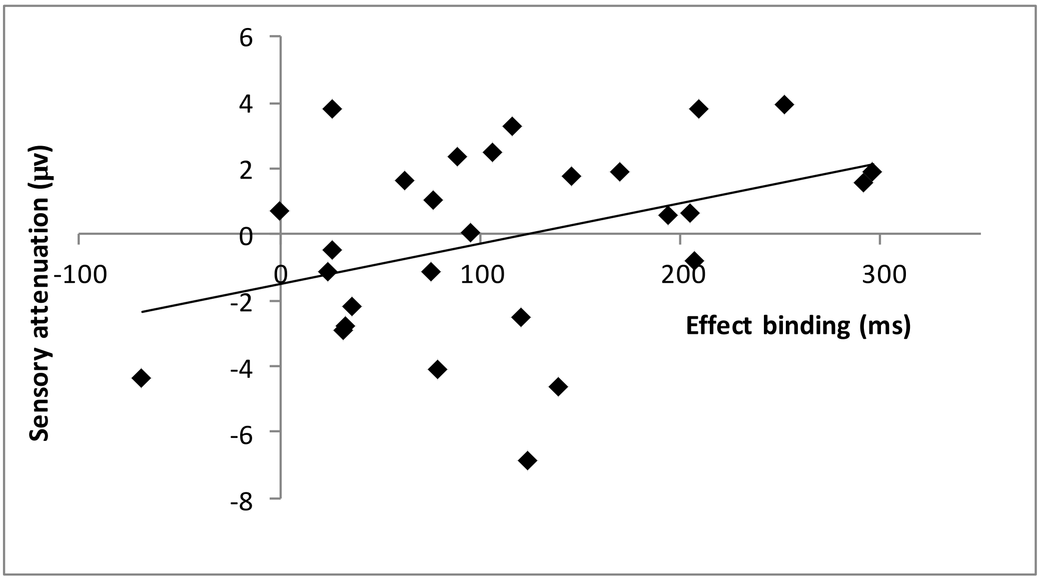
Figure 5.6 Auditory-Evoked Potentials for the Sound Condition (S) and the Operant Sound Condition (SO), Grand Averages



Repeated measures ANOVA was conducted with four time intervals (0-100ms, 100-200ms, 200-300ms and 300-400ms) and two conditions (S vs. SO) as within-subjects variables. Mauchley's test of Sphericity was significant, so Greenhouse-Geisser corrections were applied. The ANOVA demonstrated a main effect of condition (S vs. SO), $F(1, 28) = 9.62$, $p = .004$; and of time interval, $F(4, 84) = 84.7$, $p < .001$; as well as an interaction $F(3, 81) = 29.4$, $p < .001$, (Figure 5.4). Paired samples *t* tests showed that the amplitude of the auditory-evoked potentials differed significantly in each of the three time intervals 100-200ms, 200-300ms and 300-400ms, $p < .03$. The auditory-evoked potential in the SO condition had a less negative amplitude in S than SO, in time interval 100-200ms; and less positive amplitude, in time intervals 200-300ms and 300-400ms, reflecting attenuated auditory processing of the self-generated sound.

In order to explore the sensory attenuation of N1, the interval 140-170ms was selected (following van Elk, Lenggenhager, Heydrich, & Blanke, 2014). In this time interval, effect binding correlated with sensory attenuation, measured as the difference between the amplitude of N1 in conditions S and SO, *r* = .38, *p* = .04, confirming hypothesis (v) (Figure 5.5).

Figure 5.7 Scatterplot for the Correlation between Effect Binding and Sensory Attenuation



Interoceptive accuracy, however, was not correlated with sensory attenuation (measured as the difference between the amplitudes of N1 in S and SO in the interval 140-170ms), *r* = -.04, *p* = .83, contrary to hypothesis (vi). Nor was interoceptive accuracy correlated with the mean amplitudes of either evoked potential in this time interval: in condition S, *r* = .19, *p* = .32; and in condition SO, *r* = .26, *p* = .19.

Table 5.3 Multiple Regression (entry method) with Effect Binding as the Dependent Variable

Predictor	Adjusted R^2 (Sig.)	ΔR^2	β
Step 1			
Sensory Attenuation			.39
(Sig.)			(.04*)
	.12		
	(.04*)		
Step 2			
Sensory Attenuation			.41
(Sig.)			(.02*)
Interoceptive Accuracy			.40
(Sig.)			(.02*)
	.26	.14	
	(.01**)		
Step 3			
Sensory Attenuation (SA)			.41
(Sig.)			(.02*)
Interoceptive Accuracy (IA)			.40
(Sig.)			(.03*)
Interaction of SA and IA			-.06
(Sig.)			(.75)
	.26	0	
	(.03*)		

**significant at the 5% level*

***significant at the 1% level*

The various relationships between effect binding, sensory attenuation and interoceptive accuracy were explored further using multiple regression (entry method). Interoceptive accuracy and the sensory attenuation of the N1 component (measured as the difference in the amplitudes between the two conditions, S and SO, for the interval 140-170ms) together accounted for 26% of the variance in effect binding (Table 5.3). Power was calculated, post hoc, for the given parameters, which are sample size = 28, two regressors, $r^2 = .26$ and α level of .05, using a statistical table (www.statstodo.com/SSizMReg_Pgm.php), which indicated power = .74. A sample size of 33 would be required for the more generally recommended level of power = .8. These two regressors appear to have independent influence, as their interaction did not add to the explanatory power of the model. The time modulus measure was added to the multiple regression, as a potential confound. This had no significant effect and did not improve the explanatory power of the model.

5.1.4 Discussion

Intentional binding was calculated using the Libet clock method and the Haggard task with operant actions. Readiness potentials and auditory-evoked potentials were recorded with EEG. Participants were required to make judgments about timing in six conditions. These were: M when they had made a spontaneous key press; W when they had first felt the urge to move; S when they had heard a computer-generated sound; plus three further operant conditions in which the key press was followed by a sound and the timing judgments required were: MO when they had pressed the key; WO when they had felt the urge to move; and SO when they had heard the sound caused by their action. Intentional binding was calculated from the behavioural data as the sum of effect binding (S - SO) and action binding (MO - M) (Haggard et al., 2002). Interoceptive accuracy was positively correlated with intentional binding and this was wholly concentrated in effect binding. In the operant sound condition (SO) only, the amplitude of the early readiness potential (-2300ms to -800ms, before the key press) was correlated with effect binding, replicating a recent report by Jo et al. (2014). Action binding was not linked to the amplitude of either the early or the late readiness potential in any condition. There was no link between interoceptive accuracy and action binding. Interoceptive accuracy was not related to the judgment of when participants felt the urge to move (W or WO), nor to the amplitude of the readiness potentials in conditions W or WO, indicating that the awareness of internal bodily cues indexed by interoceptive accuracy does not impact on awareness of the preparation of a movement. Effect binding was correlated with sensory attenuation, measured as the difference in amplitude of the N1 component of the auditory evoked potential between the sound only (S) and operant sound (SO) conditions, in the interval 140-170ms post stimulus onset, confirming reports that the two are equivalent measures of agency (Wolpe &

Rowe, 2014). Moreover the auditory-evoked potential produced by the self-generated sound peaked significantly earlier than for the identical computer-generated sound. This is in accordance with a theory that an action primes the representation of its predicted sensory consequences and thus increases the excitability of its neural representation (Waszak et al., 2012), so that the expected tone reaches the threshold of detectability earlier (Wolpe et al., 2013). Interoceptive accuracy and sensory attenuation were not correlated but together accounted for 25% of the variance in effect binding.

There are a number of potential explanations for these findings. Importantly in this experiment, interoceptive accuracy was correlated with effect binding and not with action binding, which depend on separable processes (Haggard, 2008; Wolpe et al., 2013). Feelings of agency rely on both predictive and postdictive (reconstructive inference) cues, which are motor and sensory (Moore et al., 2009). In contrast to action binding, effect binding potentially depends on the predicted exteroceptive consequences of the action and is linked to sensory attenuation (Waszak et al., 2012; Wolpe et al., 2013). It can therefore be assumed that interoceptive accuracy modulated effect binding through the predicted sensory consequences of the action.

The underlying bases of action binding and effect binding remain unclear (Wolpe et al., 1013). Effect binding appears to rely on predictive processes, whereby a signal is sent from the pre-SMA, carrying information about the expected sensory consequences of the action (Moore et al., 2010). This signal is an activation of the learned SR bond between an action and its sensory effects. Expectations therefore powerfully influence the sense of agency, by modulating the extent to which these associative bonds are activated (Moore & Fletcher, 2012). It has been proposed that this signal from the pre-SMA preactivates sensory processing, so that the predicted auditory consequences (in this experiment) reach the perceptual threshold more rapidly (Waszak et al., 2012).

That interoception necessarily plays a role in movement is implicit in the evolutionary purpose of action, which is to meet homeostatic needs and/or fulfil Darwinian drives. Many freely chosen actions in the real world are selected for their important interoceptive consequences (Quattrocki and Friston, 2014). A person's sense of agency will rely on the stimulus-response bonds that they learn, between actions and their interoceptive as well as exteroceptive consequences. Curiously, some people seem to have a stronger sense of agency than others, as evidenced by - as yet unexplained - individual differences in intentional binding (Wolpe et al., 2013). Potentially, people with high interoceptive accuracy may, over their lifetimes, develop stronger action-effect associative bonds than those in whom interoceptive accuracy is low, because these individuals have the regular benefit of salient input about the self-specifying, interoceptive effects of all their actions. These people may therefore have generally stronger action-effect bonds and hence habitually greater feelings of agency, which could influence the results in this experiment, despite the limited interoceptive consequences of the particular button pressing action. People with poor interoceptive accuracy, by contrast may have weaker input from the interoceptive consequences of their actions and therefore experience a generally less strong sense of agency. Although highly speculative, such an explanation might account for the results of Experiment 6 and merits further investigation.

Potentially, the ability to judge time might also play a role in these findings. Hughes and colleagues have criticised the intentional binding paradigm used in this experiment because it cannot distinguish between the participant's ability to predict when a sensory event will occur ('temporal prediction') and their ability to use their own action to predict/control when the event will happen ('temporal control') (Hughes et al., 2013). It has been shown that attention to interoceptive processes improves the retrospective estimation of time (Pollatos, Laubrock, & Wittmann, 2014). Further research is, therefore, required to establish whether the link between interoceptive accuracy and effect binding in Experiment 6 might be mediated by individual differences in the perception of time (Meissner & Wittmann, 2011). However, effect binding relies on the judgement of the timing of a sensation that has been produced by one's own action, whereas the reported links between interoceptive accuracy and timing relate to an individual's accuracy in explicitly judging the length of an elapsed interval. This explanation therefore seems unlikely, given that the time modulus measure in this experiment had no influence on the relationship between interoceptive accuracy, effect binding and sensory attenuation (Table 5.3).

Postdictive, top-down, motivational and emotional priors linked to interoceptive accuracy, such as mood or how the participant construed the social context, might have influenced the results presented here (Synofzik et al., 2008b). Where links have previously been found between interoceptive accuracy and variables such as memory or intuitive decision-making, the effects can often be attributed to the association between interoceptive accuracy and emotional arousal (Dunn, Galton, et al., 2010; Pollatos & Schandry, 2008; Wiens, 2005). Feelings of agency are also modulated by affective state (Synofzik et al., 2008b). Thus, effect binding is stronger when outcomes are positively emotionally valenced or are associated with a monetary reward (Takahata et al., 2012; Yoshie & Haggard, 2013). Moreover, 'affective style', which describes an individual's ability to regulate emotion, also influences feelings of agency, for example in depersonalisation disorder, which is characterised by emotion suppression, reduced feelings of agency and low interoceptive accuracy (Gentsch & Synofzik, 2014). It was consequently important that the simple Libet task used in Experiment 6 had neutral cues without affective significance. The positive correlation found between interoceptive accuracy and intentional binding in this study is therefore unlikely to be mediated by emotion but more probably depends on the role that interoception plays in delineating the self. This role is predicted by the theoretical literature that links interoception with the experience of selfhood but has rarely been subject to empirical investigation (Craig, 2010; Seth et al., 2011). It is unlikely that the results depended on enhanced motivation amongst people with high interoceptive accuracy, as this would have been observed in increased amplitude of the readiness potential, which is influenced by the level of intentionality of the participant (Shibasaki & Hallett, 2006).

It is similarly unlikely that interoceptive accuracy had its effect on intentional binding through predictive motor processes at the pre-conceptual level (Wolpe & Rowe, 2014). This would have impacted on action binding, or on the amplitude of the late readiness potentials in condition M or MO, which was not observed in this experiment. Similarly, the timing of the urge to move (the W judgement) was not linked to interoceptive accuracy. These results therefore tend to confirm the findings of Experiment 4 and 5, which concluded that interoceptive accuracy does not modulate the preparation of action in these types of button-pressing paradigms where the interoceptive consequences of the action are small.

The experiment had a number of limitations. Variables not measured included anxiety, schizotypy and the ability to divide one’s attention between competing cues, which have top-down modulating effects on intentional binding or on interoceptive accuracy (Matthias et al., 2009; Moore & Fletcher, 2012; Wolpe & Rowe, 2014). The experiment was potentially underpowered, with a large number of error trials caused either by movement artefacts, or by participant’s failure to follow instructions. While 40 trials are sufficient to extract readiness potentials, more are recommended for auditory-evoked potentials (Luck, 2005; Roussel et al., 2013). However, it is unlikely that this would account for the absence of any link between interoceptive accuracy and sensory attenuation.

5.1.5 Conclusion

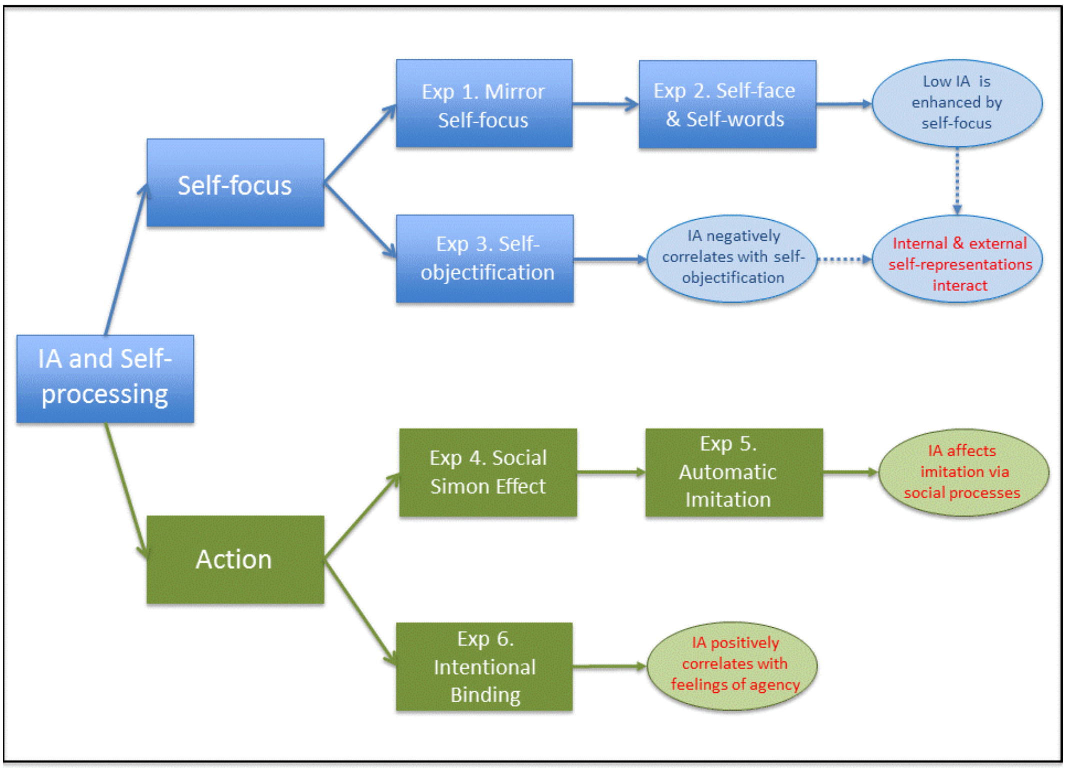
Interoceptive accuracy, measured by heartbeat perception, correlated with effect binding, measured as the perceived shift in timing of a self-generated sound towards the key press that caused it, compared with a condition in which the tone was computer-generated. Effect binding was correlated with the amplitude of the early readiness potential (from -2300 to -800ms with respect to the action), in the operant sound condition, confirming a recent report (Jo et al., 2014). However, interoceptive accuracy was not correlated with the amplitude of the early or late readiness potential in any condition of the experiment, implying that heartbeat perception does not modulate the preparation of action in this experimental context. Effect binding correlated with the sensory attenuation of self-generated sound for the N1 component of the auditory-evoked potential, defined as the difference between the amplitude around the N1 peak in the two sound conditions. However, interoceptive accuracy was not related to this measure of sensory attenuation. The results may be explained if people with high interoceptive accuracy habitually attend to the interoceptive consequences of their actions. These would then be a source of additional input to the SR bonds that individuals learn between their actions and the resultant effects, which could lead to a stronger general sense of agency in people with high interoceptive accuracy.

Chapter 6. Discussing Interoceptive Accuracy and Aspects of Self-processing

6.1 Summary

The purpose of the experiments presented in this thesis was to investigate how interoceptive accuracy, measured by the Mental Tracking Method (Schandry, 1981), modulates aspects of self-processing. The research was based on the fundamental assumption that the interoceptive senses provide a set of (often neglected) sensory inputs in contexts that rely on multisensory and/or sensorimotor integration. This characterisation of interoception reflects the early work of anatomists such as Sherrington and Pavlov, who demonstrated the presence of receptors within the body, showing that they affect emotion, behaviour and cognition, with or without awareness (Ádám, 2010; Cameron, 2002; Sherrington, 1899; Vaitl, 1996). The experiments fall into two strands. The first three considered how interoceptive accuracy interacts with exteroceptive attention to the self, while the latter three investigated whether movement preparation, agency and self/other distinction in the domain of action are modulated by interoceptive accuracy (Figure 6.1).

Figure 6.1 Overall Schematic Diagram of the Experiments and Principal Conclusions of this Thesis (principal conclusion are in red font).



6.1.1 Investigating the Interaction of Interoceptive and Exteroceptive Representations of the Self

It was assumed throughout this thesis that the self is a sensorimotor process (Ruby & Legrand, 2007) which is the product of multiple inputs in different modalities (Apps & Tsakiris, 2013). As the interoceptive senses are uniquely self-specifying (Legrand & Ruby, 2009), they are potentially important in helping to distinguishing ‘self’ from ‘other’. It has been established that interoceptive and exteroceptive representations of the self interact in body ownership, which is a fundamental aspect of self (Aspell et al., 2013; Suzuki et al., 2013; Tajadura-Jiménez & Tsakiris, 2013; Tsakiris et al., 2011). It was therefore hypothesised that heightened attention to exteroceptive aspects of the self would interact with interoceptive representations in other experimental settings. The potential for such interaction was the subject of Experiments 1, 2 and 3 (Figure 6.1).

Experiment 1 drew on a manipulation commonly employed in social psychology, where self-awareness has been studied in terms of self-focus. An early experiment (Weisz et al., 1988) reported that the accidental presence of a mirror improved performance on one, but not on another, measure of heartbeat perception. Experiment 1 employed instructed and controlled use of a mirror to heighten attention to the self, with a relatively large, heterogeneous sample of participants. Interoceptive accuracy in a baseline condition, where participants looked at a blank screen, was contrasted with the same measure while they gazed at their face in a mirror. Results demonstrated that mirror self-observation increased the heartbeat perception scores of people who had below median interoceptive accuracy in the baseline.

It was not clear whether the effect in Experiment 1 relied on real time self-observation or could be induced with a still self-photograph. Moreover, models of the self typically discriminate between ‘bodily’ and ‘narrative’ selves (Damasio, 2010; James, 1890). Within that tradition, it has been assumed that a mirror enhances attention to bodily aspects of the self. However, according to both predictive coding accounts of the self (Apps & Tsakiris, 2013) and the ‘perceptual accuracy hypothesis’ (Silvia & Gendolla, 2001), any type of heightened self-focus will improve the accuracy of judgments about the self. Experiment 2 therefore tested whether heartbeat perception could be improved by stimuli designed to enhance attention to narrative aspects of the self. Participants performed the Mental Tracking task in three conditions. In the baseline they gazed at a blank screen; in the ‘self-face’ condition they looked at a photograph; and in the ‘self-relevant words’ condition they saw self-generated words, that were designed to enhance attention to narrative aspects of themselves. Both experimental manipulations raised interoceptive accuracy, compared with the baseline. Similarly to Experiment 1, the effect was concentrated in people whose scores in the baseline were below the median value for interoceptive accuracy generally reported in large samples.

An essential aspect of human self-awareness, invoked by self-focus, is the ability to perceive ourselves as the object of our own and other people’s perception (Duval & Wicklund, 1972). In the original literature on ‘self-objectification’ Fredrickson and Roberts proposed that women’s tendency to prioritise awareness of their bodies from a third-person, objectified perspective accounts for reported gender differences in interoceptive accuracy (Fredrickson & Roberts, 1997). Experiment 3 tested this hypothesis, examining whether the tendency for women to self-objectify is related to their interoceptive accuracy measured by heartbeat perception. Results indicated that scores for heartbeat perception, together with Public and Private Body Consciousness (Miller et al., 1981), accounted for a substantial proportion of the variance in reported Self-objectification. Awareness of their bodies from within appears to give women some protection against self-objectification.

The results of Experiments 1 to 3 contribute to a growing literature showing that interoceptive and exteroceptive representations interact. They support the concept that the interoceptive senses provide a crucial set of self-specifying input in multisensory contexts (Aspell et al., 2013; Suzuki et al., 2013; Tsakiris et al., 2011). However, the possible impact of interoceptive senses in the action system has previously been ignored. Experiments 4, 5 and 6 were accordingly designed to probe the effect of interoceptive accuracy on self/other distinction in the action system, employing three classic experimental paradigms (Figure 6.1).

6.1.2 Interoception and the Action System

A growing body of research demonstrates that the interoceptive senses contribute to the multisensory integration that underpins body ownership. However, interoception must have impact in the action system, given that the fundamental basis of all action is to fulfil an organism's homeostatic goals and drives which are signalled interoceptively (Craig, 2010; Damasio, 2010). Recent theoretical accounts of action propose that movement is coded in terms of its sensory consequences (Catmur et al., 2009; Karl Friston, 2009; Hommel, 2009; Schütz-Bosbach & Prinz, 2007). That this must include the interoceptive consequences of action appears to have been largely overlooked (Heyes & Bird, 2007). The aim of Experiments 4, 5 and 6 was to explore the potential role of interoception in the domain of action. Three well-established paradigm were selected, that relate respectively to joint action, the involuntary imitation of an observed action and volition (freely chosen action).

In joint action, people must represent their own action and that of the coactor, while maintaining the distinction between self and other. Experiment 4 employed the 'social Simon task' to investigate whether the modulating effects of interoceptive accuracy on self/other overlap in body ownership illusions would extend to joint action. All participants performed the Simon task in three conditions, with two sets of stimuli, which were pictures of hands and arrows. In the 'two-choice' condition they responded with both hands (e.g. right for red cues and left for green) by making a key press when they saw a colour cue (e.g. red), while ignoring an irrelevant aspect of the cue, which was the direction (right or left) in which the stimulus was pointing. The 'Simon effect' refers to the robust finding that people are faster on trials where the directional cue is congruent with the colour cue (e.g. red points right) and slower on incongruent trials (Simon & Berbaum, 1990). This reaction time difference is termed the 'congruency effect' (Hommel, 2011). In the 'individual' condition participants responded with the right hand only to one colour (e.g. red). No congruency effect is anticipated in this condition. In the crucial 'social' condition they again responded with only their right hand (e.g. to the red cues) while a coactor now sat on their left and responded to the other colour cues. In this social condition a congruency effect has been observed and is known as the 'social Simon effect' (Natalie Sebanz et al., 2003). It has been attributed to participants involuntarily representing the motor program of the confederate. The effect is therefore potentially a measure of self/other overlap in the domain of action. It was hypothesised that participants with high interoceptive accuracy would make better self/other distinctions and would therefore demonstrate a smaller social Simon effect. However, no significant relationships were found, either because the social Simon task is flawed and is confounded by spatial distraction (Dolk et al., 2011), or because interoceptive accuracy does not modulate self/other distinction in this context.

Experiment 5 employed a further measure of self/other distinction in the action system. The congruency effect in 'automatic imitation' was measured using a well-validated paradigm (Brass et al., 2001). Participants were required to lift either their index (1) or middle (2) finger when they saw the numeral 1 or 2 respectively. These numerals appeared against the background of a videoed hand, which performed finger-lifting actions that might be congruent, incongruent or neutral with respect to the required action. The congruency effect was calculated as the difference between the participant's (faster) reaction times on congruent trials, where the numeral (e.g. 2) corresponded to the finger (i.e. middle) that the participant was required to lift, versus reaction times on incongruent trials. Smaller congruency effects have been found with enhanced self-focus and the task is thought to index the ability to make self/other distinctions (Spengler et al., 2010). It was hypothesised that good heartbeat perceivers would demonstrate better self/other distinction and hence smaller congruency effects. Surprisingly, high interoceptive accuracy was correlated with *larger* congruency effects and this was entirely accounted for by incongruent trials, indicating that it depended on 'output modulation' by some unidentified social top-down effect (Heyes, 2011). There was no relationship between heartbeat perception and reaction times on congruent trials, indicating that interoceptive accuracy did not modulate the preparation of action in this experiment.

For Experiment 6, a paradigm was chosen that specifically separates sensory and action effects and includes EEG recording of readiness potentials and auditory-evoked potentials. The experiment investigated whether interoceptive accuracy modulates 'intentional binding' (Haggard, Clark, & Kalogeras, 2002), using the classic Libet clock (Libet et al., 1983). Participants made spontaneous key presses, in six blocked conditions, and reported the following judgments: W when they had first felt the 'urge' to move; M when they had made a key press: WO when they had felt the urge to move in an operant condition that resulted in a tone; MO when they judged that they had made the key press in the operant condition; SO when they had heard the tone in the operant condition; and finally, in a condition without movement by the participant, S when they had heard a randomly generated tone. From the behavioural data, intentional binding was calculated as the sum of 'effect binding' (S - SO) (indicating how the sound in the operant condition was perceived as shifted towards the key press) and 'action binding' (MO - M) (indicating how the perceived time of the button press in the operant condition was shifted towards the sound). Interoceptive accuracy was positively correlated with intentional binding and this was wholly accounted for by a correlation with effect binding. Interoceptive accuracy was unrelated to the amplitudes of the readiness potentials (RPs) in any condition, indicating that the preparation of the action was not affected by heartbeat perception scores. However, in the operant sound condition, the amplitude of the early RP (from -2300ms to -800ms, with respect to the button press) correlated with effect binding, replicating a recent report (Jo et al., 2014). Moreover, the behavioural measure of effect binding (S - SO) was correlated with sensory attenuation of the tone, measured as the difference between the amplitude of the auditory-evoked potentials in the sound (S) and operant sound (SO) conditions, in the intervals 140-170ms, which included the peak of the N1 component (van Elk et al., 2014). Together interoceptive accuracy and sensory attenuation explained a significant portion of the variance in effect binding. However, these two predictors were not inter-correlated and appear to act independently. An outline of the six experiments and the principal findings of this thesis are shown in Figure 6.1. In this diagram ellipses represent the results of the experiments. Principal conclusions are in red font.

6.2 Methodological Issues

6.2.1 Confounds of Heartbeat Perception Tasks

Heartbeat perception tasks are reportedly confounded by gender, body mass index (BMI) and cardiovascular parameters (Ádám, 2010; Vaitl, 1996). Moreover, these factors potentially interact, for example, women generally have more body fat and smaller hearts than men (Jones, 1995). Performance on the Whitehead method of heartbeat perception (Whitehead & Drescher, 1980) declines with age (Khalsa, Rudrauf, & Tranel, 2009), possibly through reduced fitness, although this result has not been reported for the Mental Tracking Method.

A large number of people were tested using Mental Tracking during the experiments presented in this thesis (see the Appendix). Gender, age and resting heart rate were available for all these individuals. In most experiments, participants reported their weight and height, from which body mass index (BMI) was calculated. This data was analysed to examine the potential impact of confounds on the experimental findings (discussed in the Appendix).

A robust and reliable finding, across all studies, was that heartbeat perception and resting heart rate were negatively correlated, in both genders, indicating that slow hearts are more easily counted. This was seen in almost every experimental sample and is likely to depend on cardiovascular variables, such as the larger stoke volume associated with a slower heart.

There were no gender differences in interoceptive accuracy, BMI, or the ability to estimate elapsed time, although men had significantly slower (possibly larger) hearts. In males only, there was a positive correlation of self-reported BMI and interoceptive accuracy but this became nonsignificant when heart rate was partialled out because higher BMI was associated with a slower heart rate in men.

In this large data set, the correlation between age and interoceptive accuracy measured by the Mental Tracking Method was nonsignificant. Potentially the difference between this result and that reported using the Whitehead method (Khalsa, Rudrauf, & Tranel, 2009) is that the latter task relies on the integration of an interoceptive signal (the heartbeat) with exteroceptive signals (a set of tones), which may become more difficult with age.

6.2.2 Validity of the Mental Tracking Method

The Mental Tracking Method (Schandry, 1981), used throughout this thesis, has been subject to considerable criticism. In particular, it has been suggested that participants guess their heartbeats by counting seconds (Brener & Ring, 1995; Dunn et al., 2010; Ring & Brener, 1996). In Experiments 4, 5 and 6, participants were asked to estimate the length of short intervals of elapsed time, from which a 'time modulus' measure of accuracy was calculated (Dunn et al., 2010).

If people perform the Mental Tracking Task by simply counting seconds, they could be expected to be accurate (and thus to be apparently good heartbeat perceivers) if their heart rates happen to beat at around 60bpm i.e. if their hearts are slow. During the task, individuals almost always count fewer than the correct number of heartbeats, which might tend to support this interpretation. In this large data set the time modulus measure was positively correlated with interoceptive accuracy, which could imply that people were counting elapsed time in the Mental Tracking task. Partial correlations showed that when heart rate was controlled, interoceptive accuracy and the time modulus continued to be correlated.

The time modulus measure and the participant's resting heart rate were therefore treated as potential confounds of interoceptive accuracy throughout the experiments presented in this thesis. This is discussed further in the Appendix. These confounds could not, however, account for the changes in interoceptive accuracy observed in Experiments 1 and 2, where they would have applied equally in all experimental conditions. In Experiment 3, heart rate and the interaction of heart rate and interoceptive accuracy were added as extra regressors but contributed nothing to the power of the regression model in explaining self-objectification. In Experiment 4, confounds of heartbeat perception are unlikely to have been responsible for the failure to find any significant effect of interoceptive accuracy on the social Simon effect, which more probably depended on the flawed experimental paradigm. In Experiments 5 and 6, resting hearts rates and the time modulus measure (and the interactions of these variables) were entered as additional regressors in all multiple regression equations but had no significant effect on the results.

6.2.3 Limitations of Applicability to other Interoceptive Modalities

An important limitation of the results presented in this thesis it that it has not been established that awareness of heartbeats correlates reliably with the ability to detect interoceptive signals in other interoceptive modalities. Two studies have found links between heartbeat perception and visceral sensation (Herbert, Muth, Pollatos, & Herbert, 2012; Whitehead & Drescher, 1980, but see also Horing, Kugel, Brenner, Zipfel, & Enck, 2013). However, no relationship has been reported between heartbeat perception and signals from the respiratory system (Harver et al., 1993). The results presented in this thesis must therefore be interpreted primarily in relation to interoceptive signals from within the cardiovascular system.

6.3 Implications for the Role of Interoception in Self-processing

6.3.1 Summary Conclusions from Experiments 1, 2 and 3

Taken together, the results of Experiments 1, 2 and 3 extend the literature that demonstrates interactions between exteroceptive and interoceptive representations of the self at the sensory level. They support the theory that interoceptive signals contribute to the multisensory integration that underpins the self. Importantly, Experiment 3 implies that trait interoceptive accuracy indexes the reliability and salience of interoceptive cues and can be characterised as the capacity for, and habit of attention to, interoceptive signals.

6.3.2 Summary Conclusions from Experiments 4, 5 and 6

Experiment 6 provided further support for the conclusion that interoception contributes to the integration of self-relevant information from many sensory modalities. There was a significant correlation in that Experiment between high interoceptive accuracy and judgment of the timing of the tone caused by the participant’s action, implying that interoception impacts on judgements that rely on activating SR bonds between an action and its predicted sensory consequences.

In marked contrast to the role of interoceptive accuracy in distinguishing self from other in contexts that rely on the multisensory integration, the results of Experiments 4 and 5 imply that people with good heartbeat perceivers do not make better self/other distinctions in the motor domain. Moreover, the EEG evidence in Experiment 6 demonstrated that interoceptive accuracy was not linked to the preparation of action, in any condition, as indexed by the amplitude of the readiness potentials. Furthermore, at the behavioural level, Experiment 6, found no correlation between interoceptive accuracy and action binding.

However, the modulating effect of interoceptive accuracy on self/other distinction has previously been demonstrated only in body ownership paradigms, where the engagement of autonomic factors (which are coded interoceptively) has been clearly shown (Barnsley et al., 2012; Ehrsson et al., 2007; Moseley et al., 2008). A possible explanation for the failure to find any modulation of action by interoceptive accuracy in Experiments 4, 5 and 6 is that the actions involved in these studies did not have sufficiently strong interoceptive effects. Actions that have significant interoceptive consequences are potentially limited to those that fulfil drives, maintain homeostasis or involve substantial social interaction (Quattrocki & Friston, 2014). An example is given by Katkin and colleague's masked fear conditioning experiment, where electric shocks were used to give some of the stimuli interoceptive consequences (Katkin et al., 2001), with the result that the ability of participants to discriminate between stimulus type was modulated by the individual's interoceptive accuracy. By contrast, the interoceptive consequences of key presses in Experiments 4, 5 and 6 are likely to have been too small for individual differences to have measureable impact. Potential ways to add interoceptive effects to experimental conditions is discussed further in section 6.5 below.

The evidence from all the successful experiments presented in this thesis can be explained if good heartbeat perceivers are people who habitually attend to and weight their interoceptive signals, potentially at the expense of attention to exteroception. This idea is fundamental to the predictive coding model presented below.

6.4 A Predictive Coding Account of Individual Differences in Interoceptive Accuracy

Why people can detect their heartbeats has never been adequately explained (Verdejo-Garcia et al., 2012). According to predictive coding accounts of cortical function, heartbeat perception should scarcely be possible and the phenomenon requires explanation. The strength, rhythm, and variability of one’s own heartbeat is constantly present throughout one’s life and should therefore be fully predicted by the brain. Support for the habituation of the brain to heartbeat signals is provided by van Elk and colleagues, who recently showed that the N1 auditory evoked potential is attenuated when people are played their own heartbeats, compared with similar stimuli (van Elk et al., 2014). This is to be expected for a constantly present and predictable stimulus.

The model presented below (section 6.4.2.5) attempts to explain how heartbeat perception occurs and proposes that individual differences in heartbeat perception can be characterised in terms of individual differences in ‘precision’ in the interoceptive system. It is necessary first to outline the theoretical elements that make up predictive coding models.

6.4.1 Preliminary Predictive Coding Concepts

The predictive coding framework (Clark, 2013; Friston, 2010) provides a general model of brain function with great depth and potential explanatory power (Hohwy, 2010). Perception (Friston, 2012); action (Adams et al., 2012); attention (Feldman & Friston, 2010); and learning (Moran et al., 2013) have all been described within a predictive coding framework. Interoception has recently been added to this framework (Seth et al., 2011; Seth, 2013) but individual differences in interoceptive accuracy have scarcely been considered (Fotopoulou, 2013; Seth et al., 2011).

6.4.1.1 Free Energy

The fundamental principle of free energy is that, in order to survive, a living organism must maintain its body within a narrow range of ‘desirable’ states (K Friston, 2010; Karl Friston, 2009). It is proposed that this is achieved by minimising the sum of differences between the desired and the actual states of the body (‘free energy’), across time. It is now appreciated that interoception provides the organism with the vital models of the internal states of its body, which underpin both homeostasis and free energy minimisation (Gu & Fitzgerald, 2014).

The free energy model is operationalised using predictive coding and Bayesian inference (Friston & Kiebel, 2009; Huang & Rao, 2011). Predictive coding builds on Helmholtz’s insight that no living organism has veridical access to the true state of its environment (Helmholtz, 1860). Instead, it has to infer the hidden state of the external world from the effects that the environment has on the organism’s internal neural states, through the activity of its sensory receptors (Clark, 2013). Within predictive coding, it is proposed that incoming sensory data is compared against the brain’s probabilistic ‘prior prediction’ (best guess) about what hidden events in the environment have caused any given set of changes within the organism’s own nervous system. If the two are not compatible, ‘prediction errors’ arise between the prediction and the data and these are passed to a higher level in the cortical hierarchy for resolution.

An essential assumption is that predictive coding is hierarchical. The nature of hierarchies in interoceptive systems has yet to be fully established (Seth, 2013) but the most detailed model is provided by Critchley and Harrison (2013), who identify three pathways for interoceptive signals. One pathway conveys motivational information (e.g. hunger) and travels along the vagus nerve to the nucleus of the solitary tract. Another (often signalling tissue damage) arises in the viscera and projects by way of spinal laminar 1 to the spinothalamic tract. A third carries humoral information and influences principally circumventricular organs and the hypothalamus. All pathways converge on the insula and anterior cingulate cortices, which in turn have widespread connections with prefrontal and temporal areas. Information is potentially integrated at every level of this hierarchy as well as in the insula itself, which has a posterior to anterior gradient, whereby interoceptive information from all modalities is mapped and remapped and integrated with exteroceptive cues (Craig, 2009). It is assumed that the self is a widely distributed hierarchical percept, to which many systems contribute (Apps & Tsakiris, 2013; Limanowski & Blankenburg, 2013). Within hierarchies, only bottom-up data that is not compatible with the top-down prediction is passed to a higher cortical level, in the form of prediction error (Clark, 2013; Fiston, 2010). A percept is formed, in a ‘winner takes all’ manner (Summerfield et al., 2006), once prediction error (and thus free energy) is minimised at every level in the system. The process of forming a percept by this type of hypothesis testing is known as ‘perceptual inference’ (K Friston, 2005). The resulting percept will not necessarily be accurate but will be the best available. In exteroception the percept is often assumed to be conscious, although the process may equally be applied to interoceptive or exteroceptive stimuli that do not reach awareness (Hohwy, 2012).

6.4.1.2 Precision

An important aspect of both (top-down) prior predictions and the incoming sensory data (which gives rise to the prediction errors) is that they vary in the reliability of the information that they convey (e.g. how noisy they are). ‘Precision’ is therefore a key concept in predictive coding. All priors and prediction errors are represented probabilistically, with ‘precision’ defined as the inverse variance (the uncertainty) of the probability distribution associated with the prediction or with the prediction errors arising from the available sensory data (Karl Friston, 2009). Thus, in any modality and context, the brain makes both a ‘first-order prior prediction’ (a best guess) about what percept can best account for the incoming sensory data and also a ‘second order’ estimate of the reliability (precision) of both the prior prediction and the incoming data (Brown et al., 2011; Hohwy, 2012). Precision therefore applies weighting to prior predictions and prediction errors and determines their relative impact on the final percept. Precision is always an estimate that depends on context, previous learning and attention (Hohwy, 2012). Sensory data (and consequent prediction error) that is compatible with only a narrow range of potential priors has ‘high precision’ and thus carries information that is reliable. Its likely effect is that an imprecise prior prediction will alter to take account of precise prediction errors, in other words precise prediction errors affect the final percept. The result is a new ‘posterior prediction’. By contrast, sensory signals with ‘low precision’ are compatible with a wide range of potential prior predictions and the resulting imprecise prediction errors they set up are likely to be treated as unreliable information and consequently suppressed by (i.e. encompassed within) a precise prior (Moran et al., 2013). Precision is partly learned (Feldman & Friston, 2010) but also depends on the effect of neuromodulators (K Friston et al., 2012; Moran et al., 2013). In the interoceptive system, precision may be governed by oxytocin

(Quattrocki & Friston, 2014). Attention and precision interact reciprocally, in that people will attend preferentially to signals that their brain's estimate to be relatively precise but, conversely, attending to a particular sensory channel has the effect of increasing the precision of prediction errors in that modality (Jiang, Summerfield, & Egner, 2013).

A central aspect of predictive coding is that information from any sensory modality can be used to explain away prediction error in any other (Apps & Tsakiris, 2013). Precision is crucial when selecting amongst information in a variety of modalities because the brain preferentially weights signals that are the most precise in the current context. For example, when vision is imprecise at night interoceptive input has relatively greater precision (Pezzulo, 2013).

In order to minimise prediction error, the organism must learn over time to assign the best possible set of the weights, in other words to optimise the relative precisions of priors and prediction errors across all modalities (Fotopoulou, 2013). Although weighting prior predictions and prediction errors by their precision is an optimal strategy for reducing prediction error (and thus free energy) in the long term, it does not follow that the perceptual outcome is always accurate. Errors and illusions can be explained by inaccurate precision as well as by inaccurate predictions (Edwards, Adams, Brown, Pareés, & Friston, 2012).

6.4.1.3 Active Inference

While precise prediction errors can have the effect of updating a relatively imprecise prior prediction, they may also lead to 'active inference' (particularly if they interact with a precise prediction). Active inference describes how the organism moves to sample the environment and gain more sensory input with which to confirm, or correct, its predictions (Adams et al., 2012; Brown et al., 2011).

The central assumption of active inference is that an organism moves by forming a prediction of the proprioceptive consequences of the intended/desired action. This immediately gives rise to proprioceptive predictions errors between the current proprioceptive state of the organism and the predicted/desired proprioceptive state.

It is these proprioceptive prediction errors that crucially provide motor control, fulfilled at the lowest level by peripheral motor reflexes (Friston, 2013).

The role of attention is essential in active inference. Attention to the sensory consequences of an action (e.g. the visual, auditory, somatosensory, proprioceptive, and presumably also the interoceptive, outcomes) tends to stop the action (Brown et al., 2013). Therefore, within a predictive coding framework, sensory attenuation is explained as a transitory reduction in the precision of reafferent signals (Brown et al., 2013). This has the counterintuitive implication that the organism must temporarily withdraw its attention from the sensory consequences of its own behaviour in order for an action to happen.

6.4.1.4 Interoception within a Predictive Coding Framework

Although interoception necessarily plays a crucial role in free energy minimisation, this has only recently been discussed within this literature. An innovative model by Seth and colleagues proposes ‘interoceptive inference’ as directly analogous to perceptual inference in exterosensory systems (Seth et al., 2011; Seth, 2013). If interoceptive inference indicates that there are deviations from the desired inner state of the body, one way to resolve the consequent (precise) interoceptive prediction errors would be to update interoceptive predictions about the internal state of the body (Friston, 2013; Seth et al., 2011). However, this has limited applicability because only narrow deviations from desirable interoceptive states are compatible with life. Mechanisms equivalent to those that underlie active inference therefore come into play. For example, if body temperature falls below normal levels, the consequently precise interoceptive prediction errors result in homeostatic change, by becoming instructions that enslave autonomic reflexes (e.g. initiate shivering), in a manner exactly analogous to the way in which precise proprioceptive prediction errors cause active inference (Gu & Fitzgerald, 2014; Seth, 2013). The insula, in which the processing of interoceptive predictions and prediction errors occurs, has consequently been characterised as an extension of the sensorimotor strips into interoceptive territory (Gu et al., 2013). Precise interoceptive prediction errors can, however, have another effect. In animals that move, they may be resolved by action, such as finding shelter (Gu & Fitzgerald, 2014). Interoceptive inference is thus seamlessly linked to perceptual inference and to active inference, within the predictive coding framework.

While Seth's seminal model has clarified the role that interoception plays at the heart of free energy minimisation, there is a potential flaw. His model defines emotion as interoceptive inference i.e. as interoceptive percept. A more convincing account proposes that emotion is interoceptive prediction error. This implies that emotion indexes deviations from those desired states of the body that are consistent with the organism's Darwinian success (Joffily & Coricelli, 2013). The model below adopts this latter definition of emotion, as more in keeping with the free energy principle, as well as having better explanatory power.

An aspect of interoceptive signalling that has yet not been addressed within predictive coding models of interoception is precision, which must necessarily play as important a role in the interoceptive system as it does in perceptual inference and active inference (Hohwy, 2012). Evidence for the influence of precision in interoception is provided by studies that have experimentally enhanced attention to interoception (and thus precision). Subliminal fear conditioning, for example, is stronger after practice on a heartbeat perception task (Raes & De Raedt, 2011). Similarly, attention to heartbeats enhances insula activity during later judgments about emotional faces (Ernst, Northoff, Böker, Seifritz, & Grimm, 2013), presumably because attention increases the precision of interoceptive prediction errors, which then must be integrated with interoceptive predictions in the insula (Gu et al., 2013).

6.4.2 Accounting for Individual Differences in Interoceptive Accuracy within a Predictive Coding Framework

Predictive coding crucially dictates that if there is no prediction error there is nothing to be aware of (Hohwy, 2012). It follows that any bottom-up sensory stimulus that is fully predicted will be ignored. Crucially, this implies that when people do sense their hearts, the heartbeat is not at that moment fully predicted.

Within a predictive coding account there are four variables that could potentially account for heartbeat perception, as well as for individual differences in performance on heartbeat perception tasks. These are (i) cardiodynamics; (ii) the precision of the prior interoceptive prediction of the heartbeat; (iii) the precision of the incoming sensory data from the heartbeat; and (iv) the accuracy of the interoceptive prior prediction. The likely importance of each of these in explaining heartbeat perception is considered in turn below.

6.4.2.1 Cardiodynamics

The precision of the predicted prior heartbeat is likely to be at least partly dictated by physiology, as a function of the strength of signals arising from within the body (Craig, 2004) or, more correctly, by the salience of their cortical representation in the insula (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Pollatos, Gramann, & Schandry, 2007). Although recent research reports no difference between good and poor heartbeat perceivers in cardiac parameters at rest (Herbert et al., 2010; Herbert, Ulbrich, et al., 2007), it has often been proposed that cardiac perception is affected by physiological variable such as the stroke volume of the heart or the individual's distribution of body fat (Jones, 1995; Schandry & Bestler, 1995). In the experiments presented in this thesis, interoceptive accuracy and resting heart rate were robustly negatively correlated (see Appendix), implying that people with larger slower hearts have an advantage in Mental Tracking.

This can be explained in terms of precision. Strong bottom-up interoceptive signals are represented in the brain as more precise (Feldman & Friston, 2010) and tend to make the heartbeat innately more salient. The saliency of the heartbeat signal will, in turn, have the effect of further increasing the precision of the prior predicted heartbeat, whose unique pattern and rhythm is a constant presence for the individual. It can therefore be assumed that people with large slow hearts are more likely to have interoceptive signals that are precise.

6.4.2.2 The Precision of Top-down Interoceptive Predictions

Although interoceptive signalling is a cascade of sensory data that continually gives rise to predictions and predictions errors, this signalling is largely silent, indicating that it is generally fully predicted, unless some variable in the inner body deviates from established norms (which are the desirable and predicted bodily states). An person with high interoceptive accuracy, however, is one who perceives the small changes that arise when interoceptive states deviate from what is normal (i.e.

predicted) for that individual. This implies that good heartbeat perceivers are people with precise interoceptive predictions.

By contrast, an example of a person with low interoceptive accuracy would be a woman who goes into labour unaware that she is pregnant. Her experience can be explained if she has imprecise interoceptive predictions, such that substantial deviations from previous norms go unattended and unrecognized. An interesting digression in this respect is that regulated homeostatic variables often do not actually have the completely invariant set points that are usually assumed in arguments that invoke homeostasis (Ramsay & Woods, 2014). It is biologically sound for interoceptive set points to alter somewhat in the face of environmental demands, in a process known as ‘allostasis’. An important conclusions is that imprecise interoceptive predictions are not necessarily rare and, moreover, that the resultant low interoceptive accuracy may sometimes be of benefit to an organism.

The precision of interoceptive predictions is influenced by neuromodulation (Quattrocki & Friston, 2014) but is also likely to depend, at least in part, on learned experience of what is normal for oneself. Speculatively, this might be mediated by caregiving in infancy, where prompt and appropriate responses to an infant’s interoceptive needs (signalled within the child as interoceptive prediction errors) may scaffold the formation of associative bonds between the sensation (e.g. hunger, which indicates a prediction error) and the successful restoration of the desired interoceptive state (Quattrocki & Friston, 2014).

6.4.2.3 The Precision of Bottom-up Interoceptive Sensory Data and Subsequent Interoceptive Prediction Errors

Healthy people are not generally aware of their heartbeats (Koroboki et al., 2010). During the Mental Tracking task people sit quietly and arousal is avoided. The person’s heartbeat should therefore be fully predicted and they should not be able to hear it. What changes in the task, and must therefore be the source of the conscious awareness of the heartbeat, is that people are specifically required to pay attention to their heartbeat. Attention, in predictive coding, has the effect of increasing precision. It follows that, if interoceptive prediction errors become more precise, they can have impact by updating the already precise prior prediction of the heartbeat. A new posterior prediction is the result and thus a conscious ‘interoceptive percept’ will become available, as a result of this change. This is likely to be what underpins good heartbeat perception. However, if the prediction of the heartbeat is imprecise, then the new (precise) prediction errors will be absorbed into this imprecise prediction (Figure 6.2). There will be no updating of the prediction, so the heartbeat will not be heard, which would account for poor heartbeat perception.

Support for this argument is provided by the robust finding, within the interoception literature, that good heartbeat perceivers experience stronger emotions (Barrett et al., 2004; Dunn et al., 2010; Wiens, 2005). Emotion can be defined as deviations from the desired interoceptive state of the body, in other words in terms of interoceptive prediction error (Joffily & Coricelli, 2013). Therefore, if people with high interoceptive accuracy have precise interoceptive predictions they will be more prone to notice small deviations from these (i.e. interoceptive predictions errors) and their experience of stronger emotions, for similar objective changes in physiological arousal, is readily explained (Dunn, Galton, et al., 2010; Wiens et al., 2000).

Predictive coding, moreover, implies that while interoceptive prediction errors with low precision will be suppressed, at least some of those with high precision will be resolved, in a manner analogous to active interference (Adams et al., 2012), by descending interoceptive predictions that form reference points for the autonomic reflexes that regulate homeostasis (Gu & Fitzgerald, 2014; Seth, 2013). This implies that individuals with high interoceptive accuracy will have high autonomic reactivity to emotional stimuli, which has been reported (Ferri, Ardizzi, Ambrosecchia, & Gallese, 2013; Pollatos, Herbert, Matthias, & Schandry, 2007). Similarly, it has been shown that people with good interoceptive accuracy perform better on tests of masked fear conditioning, in which pictures of snakes and spiders are paired with electric shocks (Katkin et al., 2001). Successful detection in that task must rely on interoceptive responses to the shocks during the conditioning phase, which then produce interoceptive signals when the stimuli are presented in the test phase. Only good heartbeat perceivers are able to recognise the relevant trials above chance, implying that their interoceptive prediction errors are more precise than those of poor heartbeat perceivers.

The suggestion that good heartbeat perceivers have precise interoceptive predictions, and prediction errors, is supported by Paulus and Stein's influential 'insula model of anxiety'. They presciently proposed that anxious people 'experience an augmented signalling of the difference between the observed and expected body state' (Paulus & Stein, 2006). These words imply precise prediction errors, leading to increased autonomic reactivity. Their model is equally compatible with the accurate (precise) interoceptive prediction errors they suggest are common in anxiety as well as the 'noisy' (i.e. imprecise) interoceptive signalling sometimes reported in depression (Paulus & Stein, 2010).

6.4.2.4 The Accuracy of the Interoceptive Prediction

For completeness, it should also be noted that predictions are the brain's 'best guesses' about what accounts for the incoming sensory data and they are consequently not always accurate, although they will be optimal for that individual at a given moment. An inaccurate prior prediction should update in response to disconfirming incoming sensory data. The interoceptive predictions of healthy people are therefore likely to update to new posteriors, over time, as the brain seeks to optimise precision i.e. to assign the best possible set of weights to its predictions and prediction errors (Fotopoulou, 2013). However, a number of clinical conditions may be explained in terms of predictions that chronically fail to update. Panic disorder is an example, where a subset of people with high interoceptive accuracy have a tendency to catastrophise about harmless internal changes (i.e. prediction errors). This implies that their interoceptive prediction errors and priors predictions are both precise (so that the interoceptive change is noted) but that the consequent interoceptive prediction is inaccurate, in other words that a new and more accurate posterior has not formed (Clark, 1986; Ehlers & Breuer, 1992; Van der Does, Antony, Ehlers, & Barsky, 2000). The same may be true of specific phobia, where the sufferer avoids the fearful stimulus and so never learns to update the inaccurate interoceptive prediction that the frightening stimulus poses a serious danger (Ost, 1996).

Eating disorders are associated with low interoceptive accuracy (Herbert, Blechert, Hautzinger, Matthias, & Herbert, 2013; Pollatos et al., 2008), which can be explained in terms of imprecise interoceptive predictions that do not update. For such people, even very precise sensory data (hunger cues) may be unable to update their imprecise interoceptive predictions, which are compatible with a wide range of sensory input.

6.4.3 The Proposed Model

In interpreting the results of this thesis, it is therefore proposed that high interoceptive accuracy (measured by heartbeat perception) can be accounted for if good heartbeat perceivers have top-down interoceptive predictions (priors and posteriors) about interoceptive signals (e.g. heartbeats) that are ‘precise’. This precision is likely to be influenced by cardiodynamics but will also depend on learning and concentrations of neuromodulators. It is assumed that the effect of a heartbeat perception task is to increase attention to the bottom-up sensory data of the heartbeat. This sets up precise prediction errors whenever the sensory data deviates very slightly from the predicted heartbeat, which is also precise in good heartbeat perceivers). These precise prediction errors then update the interoceptive prior to form a new posterior percept of the heartbeat and allow this percept to temporarily reach consciousness and the heartbeat to be counted. This would also explain why the threshold of conscious reportability tends to fluctuate during heartbeat counting tasks (Ádám, 2010), as the prior prediction updates to a new posterior and is temporarily heard, until that posterior become the new prior so it is once again fully predicted and becomes unavailable to perception, before attention starts the cycle of updating again. In people with low interoceptive accuracy, by contrast, the heartbeat perception task will similarly increase the precision of the bottom up prediction errors but these are absorbed into an imprecise prior prediction about the heartbeat, which is compatible with a range of prediction errors, so that no updating of the prediction occurs and the heartbeat is consequently not heard (Figure 6.2). The results of experiments presented in this thesis can be explained within such a model.

6.4.4 Applying the Model

6.4.4.1 Bodily Self-awareness

The model is first applied to body ownership illusions because the implication that people with high interoceptive accuracy make better self/other distinctions is an important assumption in this thesis, for example in Experiments 4 and 5 and which investigate self/other distinction in the domain of action.

Body ownership can be explained within a predictive coding framework in which all representations, including the representation of self, are probabilistic (Apps & Tsakiris, 2013; Limanowski & Blankenburg, 2013). To experience the rubber hand illusion, participants must form a percept that the prosthetic hand is their own, by minimising prediction errors across all modalities. Predictive coding is a ‘winner takes all’ strategy in which only one percept is possible, as evidenced by binocular rivalry (Hohwy, Roepstorff, & Friston, 2008). The illusion that the prosthetic is part of the body appears to invoke a high level, learned prediction that seen touch and felt touch usually co-occur (Apps & Tsakiris, 2013). Attention to vision during the illusion deliberately enhances the precision of visual predictions. If interoceptive predictions are precise, however, they may serve to anchor a participant in their body, because the fake hand does not have the internal feeling of being their own. However, if interoceptive predictions are imprecise they will be suppressed in favour of the typically more reliable visual and somatosensory input, which predicts that the rubber hand belongs to them. Therefore, if low interoceptive accuracy implies low precision of interoceptive predictions, people with low interoceptive accuracy can be expected to be more susceptible to this type of body ownership illusion, as has been demonstrated (Tsakiris et al., 2011).

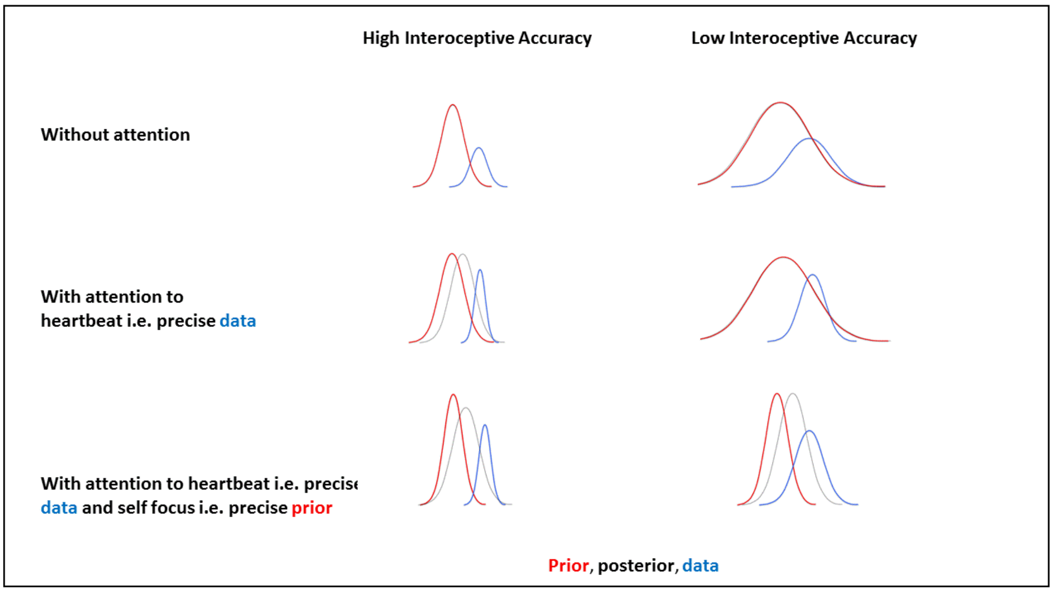
A contrasting paradigm dispenses with a prosthetic hand, by filming the subject’s true hand and replaying this to them in real time (Suzuki et al., 2013). An ‘interoceptive rubber hand illusion’ can be achieved by causing the virtual hand to flush in synchrony with the participant’s heartbeat (see Aspell et al., 2013 for a similar full body illusion). However, the interoceptive predictions in this version of the experiment now indicate that the hand is the person’s own. People for whom interoceptive predictions are precise are therefore now more, rather than less, likely to claim ownership of it, as this experiment demonstrated (Suzuki et al., 2013).

6.4.4.2 Enhanced Self-focus

Experiments 1 and 2 show that attending to self-relevant information, such as one’s own face in a mirror, a self-photograph or self-relevant words, temporarily enhances the heartbeat perception scores of people with originally below-median interoceptive accuracy (see also Maister & Tsakiris, 2014). Predictive coding models propose that the self is a multilevel construct, continually renewed in the brain from all available interacting cues, at many levels of the cortical hierarchy. Self-relevant signals in any modality, and at any level, are thus brought to bear to constitute the self. The likely explanation for the results of Experiments 1 and 2 is, therefore, that enhanced self-focus increased attention to (and therefore the precision of) high level, multi-modal prior predictions for the self (Apps & Tsakiris, 2013; Limanowski & Blankenburg, 2013). This would heighten the salience and reliability (i.e. the precision) of all interoceptive priors relevant to the self, including the heartbeat. Assuming that people with low interoceptive accuracy have imprecise prior predictions about their heartbeats, then in these people that prediction would become temporarily more precise and they would be enabled to hear their heartbeat during Mental Tracking. Good heartbeat perceivers already have precise heartbeat predictions and no effect would be observed. This is illustrated in Figure 6.2 where the probability distribution of the prior for the heartbeat (when there is no special attention to the heartbeat) is shown in red. This prior is precise (i.e. has small variance) in those people who have high interoceptive accuracy (left column) and is imprecise in those individuals for whom interoceptive accuracy is low (right column). Originally (top row), without attention to the heartbeat, the heartbeat in both sets of people is fully predicted and not heard because it falls within the probability distribution of the existing prior. The effect of paying attention to the heartbeat during Mental Tracking (middle row) is to make the incoming sensory data more precise (i.e. have less variance). In the case of people with low interoceptive accuracy (right column) the more precise sensory data still falls within the wide probability distribution for the prior, so there is no updating and the posterior is equivalent to the prior. However, for good heartbeat perceivers, the increased precision of the data means that it now falls outside the distribution of the original prior, so that the prior will update to form a posterior, which is shifted towards the new data. Any such shift of prior to new posterior means that a percept is formed and the heartbeat is heard.

The effect of enhanced self-focus (bottom row), in Experiments 1 and 2, is to increase the precision of priors for all self-relevant information, including the heartbeat. In the case of people with low interoceptive awareness (right column), attending to the heartbeat under self-focus conditions means that the probability distribution for the data now falls outside the probability distribution of the precise prior. This results in a new posterior and the effect of the shift from prior to new posterior distribution means that a percept is formed and the heartbeat is heard. Something similar happens in people with high interoceptive accuracy (i.e. the prior for the heartbeat becomes more precise) but they were already hearing the attended heartbeat, so there is no improvement in their interoceptive accuracy as a result of the self-focus.

Figure 6.2 Applying the Predictive Coding Model to Heartbeat Perception and Enhanced Self-focus



A similar enhanced self-focus mechanism may explain the report by Fotopoulou and colleagues that two somatoparaphrenic patients who were initially unable to recognise their limb as their own when viewed directly, could correctly recognise their arm when they saw it in a mirror (Fotopoulou, Jenkinson, Tsakiris, Haggard, & Rudd, 2011). Potentially, the exteroceptive (visual) representation of the body increased the precision of their interoceptive self-related predictions and resulted in improved body-awareness.

The mechanism for improved interoceptive accuracy during heightened self-focus is likely to be provided by attention-switching activity in the anterior insula. Predictive coding accounts assume that predictions about the interoceptive state of the body and prediction errors (consequent upon differences between the expected and actual bodily state) are reconciled in the insula (Gu & Fitzgerald, 2014; Seth, 2014). This cortical area is engaged in all interoceptive signalling (Cauda et al., 2011; Craig, 2010; Simmons et al., 2013), including being activated during self-face recognition (Devue & Brédart, 2011). Performance on cardiac awareness tasks correlates with activity and also with grey matter volume in the right anterior insula (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). Lesions of the insula are implicated in disorders of body awareness such as somatoparaphrenia (Baier and Karnath, 2008). From converging fMRI and diffusion tensor imaging data (Menon & Uddin, 2010), it is proposed that the insula is a hub between brain networks involved in externally-directed attention to stimuli in the environment and internally-directed attention to cortical midline structures involved in self-referential processes (Northoff, et al., 2006), a theory also endorsed by Farb, Segal, and Anderson (2012).

It is therefore probable that attention to exteroceptive self-relevant information in Experiments 1 and 2 resulted in enhanced insula activity, in the same way that attention to heartbeats enhances BOLD activity in the insula during subsequent emotional processing tasks (Ernst, Northoff, et al., 2013). Such enhancement could, in turn, facilitate other aspects of self-processing, by top-down gating of attention. The gating of attention would also explain why the experimental effects were not significant in individuals with high baseline interoceptive accuracy, who are already generally attentive to internal states of their bodies, even in the absence of any externally driven focus of attention to the self.

6.4.4.3 Self-objectification

Predictive coding accounts assume that the self is a multimodal construct, to which many systems contribute, and the brain is assumed to weight these modalities in terms of their relative precision. It is furthermore assumed, in the model presented here, that high interoceptive accuracy indicates the tendency for interoceptive predictions to be weighted as precise. This would explain why, in Experiment 3, women with high interoceptive accuracy were less liable to self-objectify. Self-objectification involves attending to one's body principally from a third-person, exteroceptive, visual perspective, rather than from an interoceptive perspective. Habitual attention to a particular channel has the effect of increasing its precision. Trait self-objectification consequently implies the woman has heightened precision of exteroceptive, at the potential expense of interoceptive predictions, about her body. The precise interoceptive predictions of women with high interoceptive accuracy are, conversely, likely to provide some protection against the tendency to attend to objectified, visual aspects of self.

6.4.4.4 The 'Social Simon Effect'

Experiment 4 was the first to consider interoceptive accuracy in the domain of action. It was assumed that action is coded in terms of its sensory consequences (Hommel et al., 2001; James, 1890), which includes interoceptive consequences (Heyes & Bird, 2007). It was therefore expected that interoceptive accuracy would add self-specifying input that would modulate self/other distinction in the social Simon task. It was anticipated that good heartbeat perceivers would experience less self/other confusion, resulting in less tendency to represent the planned action of the coactor and hence a smaller congruency effect in the social condition. No such relationship was observed.

Potentially the 'social Simon' paradigm is flawed and results only from the biasing of spatial attention towards the coactor. However, the model in section 6.4.3 proposes that interoceptive accuracy depends on the precision of interoceptive predictions (i.e. their salience, reliability) relative to predictions in other sensory modalities. It would follow that in situations with notable interoceptive consequences, such as the rubber hand illusion, good heartbeat perceivers are more able to distinguish between their true hand and a prosthetic because they have precise interoceptive predictions about their own bodies. The interoceptive consequences of the action in the social Simon task were potentially too small for any modulatory effect of interoceptive accuracy to be detected.

6.4.4.5 Automatic Imitation

In Experiment 5 it was again anticipated that people with high interoceptive accuracy would be better able to distinguish self from other. It was consequently hypothesised that they would have faster mean reaction times on incongruent trials, during automatic imitation, as observed by Spengler et al. (2010). Contrary to expectations, it was observed that good heartbeat perceivers had *slower* mean reaction times in incongruent trials, implying greater difficulty in inhibiting the tendency to automatically imitate observed actions.

Automatic imitation involves both cued movement and action observation. It had also been anticipated that interoceptive accuracy would modulate the long-term, stimulus-response bond that links the participant’s representation of their action with its sensory consequences, because interoception should contribute to the sensory outcomes of an action. However, the concentration of the effect, in Experiment 5, in incongruent cues indicates that it was fully accounted for by the action-observation aspect of the task and was not related to the cued movement and thus to ‘input modulation’, which depends on the common coding of the participant’s actions and their sensory outcomes. Analogously with Experiment 4, the likely explanation is that good interoceptive accuracy does not promote self/other awareness *per se* but has its effects through the precision of interoceptive predictions. Interoceptive accuracy can therefore be expected to modulate only those actions with marked interoceptive consequences. As in Experiment 4, the interoceptive consequences of the action in Experiment 5 were likely to have been too small to have affected the outcome.

In Experiment 5 interoceptive awareness was linked to greater ‘output modulation’, which depends on social top-down effects (Heyes, 2011). A possible explanation is that good heartbeat perceivers experience the aversive consequences of potential errors more strongly. This is demonstrated by the higher amplitude of the error-positivity response to making a mistake that has been observed in people with high interoceptive accuracy (Sueyoshi et al., 2014). Moreover, Band and colleagues have demonstrated that an error-related EEG signal, similar to that found when an error is made, is experienced when there is no actual mistake but participants experience a mismatch between the expected and the actual effect of an action – similarly to incongruent trials in automatic imitation (Band et al., 2009). A heightened aversive response in good heartbeat perceivers would lead to greater activity in the anterior insula and anterior cingulate when they experience the risk of making errors during the automatic imitation task (Preuschoff et al., 2008; Singer et al., 2009). The resulting greater response conflict would heighten activity in the insula, which could slow their reactions. This explanation is consistent with the conclusion that good heartbeat perceivers have more precise interoceptive predictions and prediction errors because this implies stronger emotions, including aversive responses (Joffily & Coricelli, 2013). The explanation thus also depends on the greater emotional arousal experienced by people with high interoceptive accuracy, which can be accounted for by the assumption that they have precise interoceptive predictions and prediction errors (Barrett et al., 2004; Dunn et al., 2010; Pollatos & Schandry, 2008; Wiens et al., 2000).

6.4.4.6 Feelings of Agency

In Experiment 6, heartbeat perception was correlated with the effect binding measure of participants' sense of agency. EEG data, however, showed that interoceptive accuracy was not related to the amplitude of either the readiness potentials or the auditory-evoked potentials. This behavioural relationship, that was not mirrored at the physiological level, is reminiscent of the relationship between interoceptive accuracy and emotion, where the behavioural measure (the self-reported strength of emotional feelings) differs between high and low heartbeat perceivers, despite there being no difference in objective measures (i.e. physiological differences in heart rate or skin conductance) Dunn et al., 2010; Wiens et al., 2000). Differences in emotion experience have been explained above in terms of precision in interoceptive systems and the same is potentially true of effect binding.

The causes of individual differences in intentional binding have yet to be elucidated (Wolpe et al., 2013) but predictions and the precision of predictions is likely to play a crucial role. The many factors that influence the sense of agency can best be explained by the 'multifactorial account' (Synofzik et al., 2013), within which cues to agency are combined in a Bayes optimal fashion, according to their reliability. Wolpe and Rowe (2014) have recast this into a predictive coding model in which the sense of agency depends on reconciling top-down predictions about the authorship of an action with the bottom-up sensory data. That effect binding is a predictive process is indicated by the manner in which it can be disrupted by theta burst TMS over the pre-SMA (Moore et al., 2010). Crucially, within Wolpe and Rowe's account, the sense of agency therefore depends on relative precision, which assigns weights to predictions and to all available incoming data, in order to arrive at the most probable cause of a sensation. If high interoceptive accuracy is explained by high precision of interoceptive cues, then good heartbeat perceivers are likely to have stronger learned SR bonds between freely chosen actions and their self-specifying interoceptive effects. However, why this should give them a stronger sense of agency over the exteroceptive (auditory) effects of their actions is not obvious.

6.5 Future Directions

The results presented in this thesis raise a number of questions. Firstly, more investigation is required to determine the underlying cause of the correlation between effect binding and interoceptive accuracy in Experiment 6. Secondly, further research is warranted before it can be definitively concluded that interoception does not impact on the preparation of action. Thirdly, the predictive coding model presented has implications that can potentially be tested. Finally, innovative new means of testing interoceptive accuracy are desirable.

The mechanisms that underpin intentional binding remain the subject of debate (Hughes et al., 2013; Moore & Obhi, 2012). The classic paradigm, used in Experiment 6, does not distinguish between a number of potentially separable effects which can be teased out using appropriate experimental controls (Hughes et al., 2013).. The results might, for example, be confounded by the participant’s ability to estimate time, which has been linked to interoceptive accuracy (Meissner & Wittmann, 2011; Pollatos et al., 2014). By contrasting a condition in which a computer generated tone occurs at a predictable (cued) time with one where the time is unpredictable (Hughes et al., 2013) it would be possible to establish whether the results of Experiment 6 indicate that interoceptive accuracy simply correlates with the ability to judge the timing of an event. Furthermore, the explanation for the results of Experiment 6 presented in section 5.1.4, implies that interoceptive accuracy may be related to sensory attenuation, which idea is supported by theoretical explanations of their linked origins (Wolpe et al., 2013) This warrants more thorough investigation with adequate numbers of trials to extract precise auditory-evoked potentials

A potential link between the results of Experiments 4 and 6 is provided by an experimental manipulation that combines intentional binding and the inhibition of action. Haggard and colleagues required participants to prepare to press a key but then (on a subset of trials) to inhibit the action at the last possible moment. Each trial was always followed by a tone. On trials where the key press was completed, the time of the tone was perceived as closer to the key press and thus the usual effect binding occurred. However, when the action was inhibited the sound was judged as occurring later than it truly had (Haggard, Poonian, & Walsh, 2009). There is scope, using this paradigm, to investigate the relationship between interoceptive accuracy and inhibition and thus to establish whether the automatic imitation results of Experiment 4 arose because good heartbeat perceivers have general difficulty inhibiting any prepared action.

It is assumed, throughout this thesis, that actions are coded in terms of their sensory consequences (Hommel et al., 2001; James, 1890), However, no effect of interoceptive accuracy on action was found in Experiments 4, 5 and 6. An experimental manipulation in which the participant’s actions have salient interoceptive consequences is required to confirm this conclusively. A variant of the Libet task, in which a key press produced a mild shock, could conclusively establish whether interoceptive accuracy modulates action binding when the action has substantial interoceptive consequences.

The predictive coding model presented above proposes that interoceptive awareness reflects sensory precision in interoceptive systems (specifically in the representation of the heartbeat). This implies that good heartbeat perceivers will weight interoceptive signals from their cardiovascular system as salient and reliable. If the model is correct, for example, good heartbeat perceivers will report less effect of a placebo (Gibbons et al., 1979). This could be tested in a variety of experimental paradigms, involving feelings (e.g. reported emotion), behaviour (e.g. reaction times) and cognition (e.g. decision making).

Finally, while two studies indicate that heartbeat perception correlates with visceral perception (Herbert, Muth, et al., 2012; Whitehead & Drescher, 1980), there has been only one report comparing respiratory resistance with heartbeat perception (Harver et al., 1993). That study found no relationship but the experiment used a signal detection method to assess heartbeat perception and such tests are not sensitive to individual differences, as most people’s performance on them is at chance (Eshkevari et al., 2014). Replication using the Mental Tracking task might be more successful. Moreover, there is scope to compare heartbeat perception with awareness in other sensory modalities that may be more closely related to interoception than exteroception. These include proprioception, which many early authorities regarded as an aspect on interoception (Ádám, 2010; Cameron, 2002; Vaitl, 1996) and the vestibular sense, which plays an important but previously neglected role in body awareness (Ferre, Vagnoni, & Haggard, 2013). The experiments presented in this thesis add to the literature showing that an individual's trait performance in heartbeat perception impacts on feelings, cognition and behaviour. However, until these effects can be shown to generalise to other interoceptive modalities, it can only be inferred that they rely on the salience of the heartbeat, rather than on a more general awareness of interoceptive sensation.

6.6 Conclusion

This thesis used the Mental Tracking Method of heartbeat perception to investigate the impact of interoceptive accuracy on aspects of self-processing, including experimental manipulations of self-focus and tests of the ability to make self/other distinction. The findings support a characterisation of interoception as a set of senses that contribute self-specifying input to multisensory integration. Enhanced attention to exteroceptive representations of both the bodily and the narrative self improved heartbeat perception in people for whom this was initially low. Good heartbeat perception in women was shown to confer some protection against self-objectification. Interoceptive accuracy did not modulate the preparation of action in any of the three experiments designed to test this. Good heartbeat perception was associated with difficulty in inhibiting the tendency to imitate an observed action and this effect depended on social top-down effects. Interoceptive accuracy modulated the sense of agency at the behavioural level, where accuracy in heartbeat perception was inversely correlated with accuracy in the perception of the timing of the auditory consequence of an action. The results can be interpreted in terms of a predictive coding model in which high interoceptive accuracy indicates high precision of interoceptive representations.

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Appendix: Investigating Potential Confounds of Heartbeat Perception in this Thesis

A large number of people were tested using the Mental Tracking Task in the course of this thesis. Putting all available data together throws light on a number of the potential confounds to heartbeat perception.

7.1 Participants

The 308 participants included students at Royal Holloway University of London and members of the public who took part in Experiment 1, hosted by the 'Who am I?' Gallery at the Science Museum, London.

7.2 Methods

The gender and age of participants were recorded and resting heart rates were available from the data collected during the Mental Tracking task. In several experiments, self-reported height and weight were requested, from which body mass index (BMI) could be ascertained. In Experiments 4, 5 and 6 participants were asked to estimate the length of several short intervals of elapsed time (19s, 37s, 49s) from which a 'time modulus' measure was calculated, this was done using a variant of the Schandry formula, {1/3 Σ [1 - (|actual elapsed time – estimated time| /actual time)]} (Dunn et al., 2010; Schandry, 1981).

7.3 Results

Taking the participants as one data set, distributions of interoceptive accuracy (IA), body mass index (BMI) and resting heart rate (HR) were approximately Gaussian. Age was skewed towards the 18-25yr age group, which included students but also constituted the majority of those who volunteered to take part in Experiment 1 in the Science Museum. The time modulus measure was highly skewed (Table 7.1).

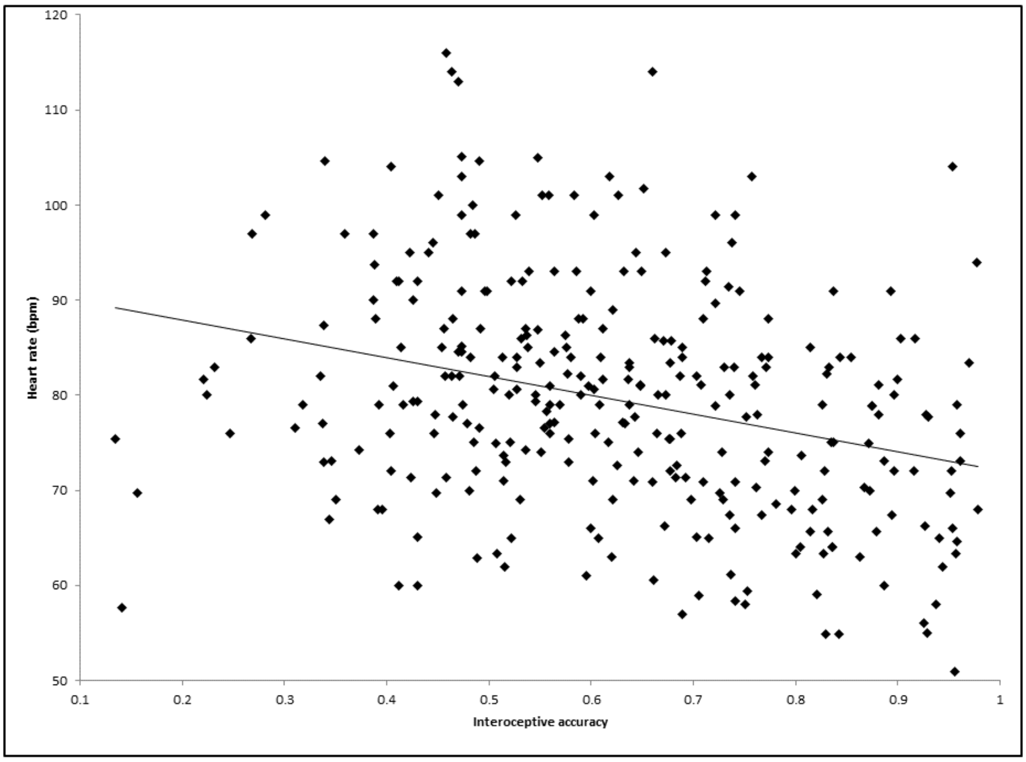
One-way ANOVA, with gender as the between-subjects variable, showed that were no differences between the sexes in interoceptive accuracy, $F(1, 306) = 1.77$, $p = .19$; in BMI (calculated from self-reported height and weight), $F(1, 289) = 0.24$, $p = .63$; or in accuracy in estimating elapsed time (the 'time modulus' measure), $F(1, 136) = 2.24$, $p = .14$. However men had significantly slower heart rates, $F(1, 306) = 4.29$, $p = .04$, which, coupled with a robust relationship between slower hearts and better performance on the Mental Tracking Task, might account for previous reports of men's better heartbeat perception.

Table 7.1 Descriptive Statistics for Interoceptive Accuracy (IA) and Potential Confounds

	Male	*Female*	*All*	*Skewness (for all)*	*Kurtosis (for all)*
IA *(SD)*	*.65* *(.18)* *n=101*	*.62* *(.19)* *n=207*	*.63* *(.18)* *n=308*	*-.04*	*-.54*
Age in years *(SD)*	*26.5* *(12.2)* *n=101*	*22.7* *(8.4)* *n=207*	*24.0* *(10.0)* *n=307*	*2.4*	*5.9*
Resting HR bpm *(SD)*	*77.5* *(11.7)* *n=101*	*80.5* *(12.4)* *n=207*	*79.5* *(12.2)* *n=308*	*.26*	*.07*
BMI *(SD)*	*22.7* *(4.6)* *n=98*	*22.4* *(3.7)* *n=193*	*22.5* *(4.0)* *n=291*	*.83*	*1.24*
'Time modulus' *(SD)*	*.78* *(.14)* *n=25*	*.72* *(.20)* *n=113*	*.73* *(.19)* *n=138*	-3.20	21.6

For the participants taken as a whole, interoceptive accuracy was negatively correlated with heart rate, $r = -.30$, $p < .001$ (Figure 7.1). This result was extremely robust and was found in almost every sample of participants (except Experiment 4) and was similar for both genders. Age was negatively correlated with heart rate, $r = -.25$, $p < .001$, which was significant for both genders, indicating that children and young people have faster heart rates than adults. Interoceptive accuracy was not correlated with age, $r = .07$, $p = .25$, for either gender (Figure 7.2). This is contrary to the reported effects of age on heartbeat perception measured by the Whitehead method (Khalsa, Rudrauf, & Tranel, 2009). Accuracy in the estimation of elasped time (the time modulus measure), however, declined with age, $r = -.23$, $p = .02$.

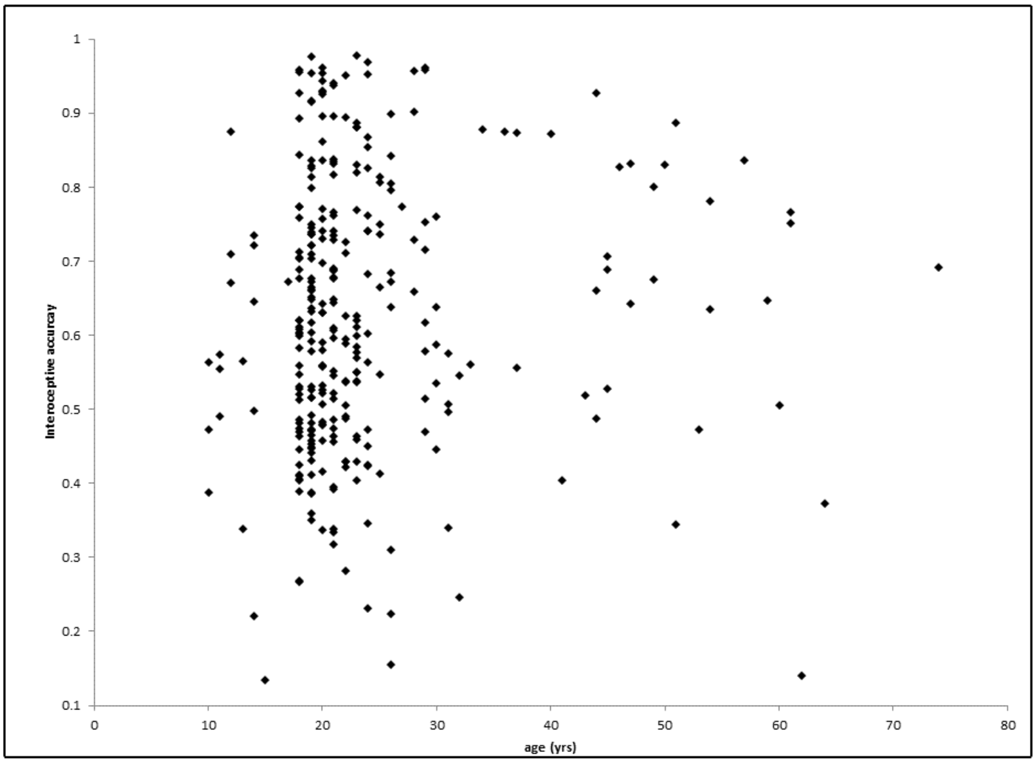
Figure 7.1 Scatterplot for Interoceptive Accuracy and Resting Heart Rate



Interoceptive accuracy was postively correlated with the time modulus measure, *r* = .30, *p* < .001. This relationship continued to be significant after controlling for the effects of resting heart rate on interoceptive accuracy, ρ = .29, *p* = .001. This might indicate that people were counting seconds rather than heartbeats on the Mental Tracking task, so the time modulus measure was treated in Experiments 4, 5 and 6 as a potential confound.

Curiously, accuracy in heartbeat perception was correlated with BMI, *r* = .12, *p* = .02, but only in males, *r* = .20, *p* = .05, and the relationship was not in the expected direction (i.e. higher BMI was associated with better, not worse, heartbeat perception). However, BMI was also negatively correlated with heart rate, again only in males, *r* = -.25, *p* = .01 (faster heart rates were associated with lower BMI in men). Partial correlation showed that when heart rate was controlled, BMI and interoceptive awarenness were no longer correlated, in males, ρ = .15, *p* = .16, or in females, ρ = .06, *p* = .41, indicating that the apparent correlation between BMI and interoceptive accuracy depended on their shared variance with resting heart rate.

Figure 7.2 Scatterplot for Interoceptive Accuracy and Age



7.4 Conclusion

The two significant confounds of interoceptive accuracy identified in this analysis were resting heart rate and the ability to estimate elapsed time (the time modulus measure). Body mass index, age and gender had no significant effect.